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Carbon burial and infill rates in small Western Boreal lakes: physical factors affecting carbon storage

Margaret M. Squires, David Mazzucchi, and Kevin J. Devito

Abstract: Effects of depression depth (Z_T), lake surface elevation (E_S), catchment area:lake surface area (A_T:A_O), trophic status, and surficial geology on sediment burial rates in small Western Boreal Plain lakes were assessed using content and chronology of cores from a relatively large and small lake on each of moraine (M), glaciofluvial (GF), and glaciolacustrine (GL) deposits. Aquatic and terrestrial plant and sediment carbon:nitrogen (C:N) suggested most buried C was aquatic. The rate of long-term total C burial averaged 31 g·m^{-2}·year^{-1} (range: 0–84 g·m^{-2}·year^{-1}); this was recently 79 g·m^{-2}·year^{-1} (range: 40–180 g·m^{-2}·year^{-1}) (higher and more variable rates than previously reported for Boreal lakes). Long-term C accrual rate and sediment depth increased with increasing Z_T. In each landform, a relatively low base elevation ($E_B = E_S - Z_T$) lake began accumulating sediment thousands of years before a high E_B lake. GF depressions were deeper and had accrued more C·m^{-2} (and infilled) faster than M and GL lakes; a large GF lake had no organic sediment, perhaps because of large groundwater inputs. Increasing A_T:A_O corresponded with increasing C accrual rates where precipitation and evaporation dominated (surface runoff infrequent) (M and GL) but not where groundwater dominated (GF lakes) lake water budgets, illustrating the importance of landform and depression characteristics in regionalizing lake-C burial estimates.

Résumé : L'étude du contenu et de la chronologie de carottes de sédiments provenant de lacs, l'un de taille relativement petite et l'autre de taille relativement grande, dans chacune des zones de dépôt de types moraine (M), glaciofluvial (GF) et glacio-lacustre (GL) nous a servi à évaluer les effets de la profondeur de la cuvette (Z_T), de l'altitude de la surface du lac (E_S), du rapport surface du bassin versant: surface du lac (A_T:A_O), du statut trophique et de la géologie de surface sur les taux d'ensevelissement des sédiments dans des petits lacs de la plaine boréale de l'Ouest. Les plantes aquatiques et terrestres et le rapport C:N indiquent que la majeure partie du C enfoui est d'origine aquatique. Le taux d'enfouissement à long terme de C total est en moyenne de 31 g·m^{-2}·an^{-1} (étendue 0–84 g·m^{-2}·an^{-1}) et à l'échelle récente de 79 g·m^{-2}·an^{-1} (étendue 40–180 g·m^{-2}·an^{-1}, des taux plus élevés et plus variables que ceux signalés antérieurement dans les lacs boréaux). Le taux d'accumulation de C à long terme et l'épaisseur des sédiments augmentent en fonction directe de Z_T. Dans chaque type de terrain, les lacs à altitude du fond ($E_B = E_S - Z_T$) relativement basse commencent à accumuler les sédiments des milliers d'années avant les lacs à E_B élevée. Les cuvettes des lacs GF sont plus profondes et accumulent plus de C·m^{-2} (et se remplissent plus vite) que celles des lacs M et GL; un des grands lacs GF ne possède aucun sédiment organique, peut-être à cause d'apports importants d'eau d'origine phréatique. Un accroissement de A_T:A_O correspond à une augmentation des taux d'accumulation de C là où le budget hydrique du lac est dominé par les précipitations et l'évaporation (avec peu d'écoulement superficiel) (lacs M et GL), mais pas où les eaux phréatiques prédominent (lacs GF); cela illustre l'importance du type de terrain et des caractéristiques de la cuvette dans l'établissement de taux régionaux d'enfouissement de C.

[Traduit par la Rédaction]

Introduction

The world's oceans and, collectively, the freshwater reservoirs, inland seas, and lakes that cover <2% of the earth's surface each accumulate 130 Tg C·year^{-1} (cf. Wurtsbaugh et al. 2003). Higher rates of C burial in lakes compared with oceans are a consequence of the lower residence times of sinking material in shallow versus deep water and better preservation of organic C (OC) as a result of lower oxygen content at the sediment–water interface in lakes than in oceans (Einsele et al. 2001).

Among lakes, small water bodies bury on average 23 Tg C·year^{-1}, whereas large lakes bury only 6 Tg C·year^{-1} (cf. Wurtsbaugh et al. 2003); across a gradient of increasing

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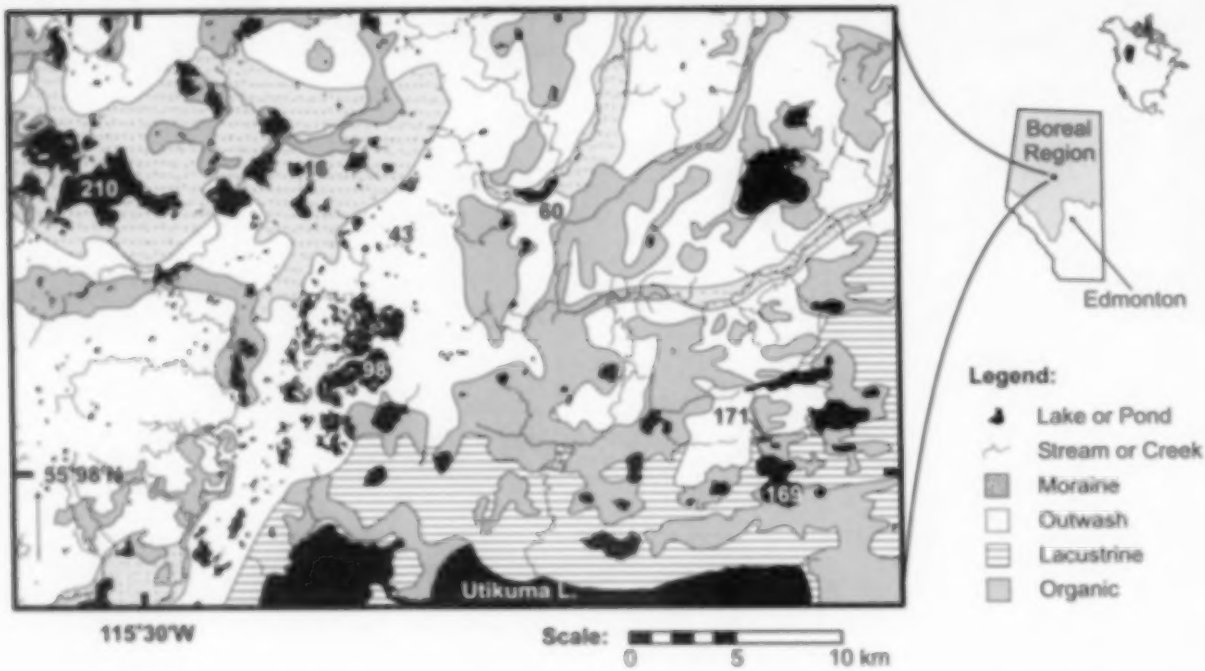
Fig. 1. Location of the study lakes in north-central Alberta, western Canada.



nutrient content of water, the rate increases from 20 to 90 $g \cdot m^{-2} \cdot year^{-1}$ in small lakes and from 5 to 20 $g \cdot m^{-2} \cdot year^{-1}$ in large lakes (Mulholland and Elwood 1982; Molot and Dillon 1996; Dean and Gorham 1998). Higher OC burial rates in small lakes have been attributed to greater catchment area to lake area ratios (A_T:A_O) compared with large lakes, since this should result in greater terrestrial organic matter inputs and nutrient loading and, as a result, higher rates of aquatic primary productivity (Mulholland and Elwood 1982; Einsele et al. 2001). However, size ultimately limits the total C storage capacity of depressions (Deevey 1955). Other physical factors that may affect the rate of C burial rate include geomorphic features of lake basins that control mixed layer depth and water residence time (Hargrave 1973, 1975; Mulholland and Elwood 1982) and landscape-level features that affect hydrologic regime, lake chemistry, and sediment properties (e.g., Dean and Gorham 1976; Swanson et al. 1988; Winter 1999). Here we describe in detail C sedimentation in a group of Alberta lakes and how environmental factors (i.e., landform–surficial geology, elevation, depression size (area and depth), A_T:A_O, hydrologic regime, and trophic status) correlate with C burial. We compare the C burial rates in our study lakes with those published for other Boreal lakes and wetlands.

Materials and methods

Study area and lakes

Prior to 1990, the study area (57°N, 115°W) (Fig. 1) was for the most part free of roads, large-scale forestry operations, and oil and gas exploration, and it remains relatively free of human influence. Physiography, climate, and vegetation are described in detail in Devito et al. (2005*a*, 2005*b*), Ferone and Devito (2004), and Bayley and Prather (2003). Briefly, the study area is underlain by Smoky Group shale, with low relief surficial deposits ranging from 50 to 100 m depth and composed of Quaternary moraine (M), glaciofluvial outwash (GF), and peat-covered glaciolacustrine (GL) sediments. About 35% of the study area is commercial forest, and 30% is peat-forming wetlands (Vitt et al. 2000). In a 13-lake survey that included six of the study lakes, depression depth (Z_T) ranged from 1 to 12 m, where Z_T = water depth (Z_W) + sediment depth (Z_S); Z_S was determined by pushing a rod to refusal at 10 locations per lake. Depression depth increased with increases in lake area up to a threshold of about 100 ha, then decreased as lake area increased (E. Jasinska, Department of Biological Sciences, University of Alberta, Zoology 812, Edmonton, Alberta T6G 2E3, unpublished data, edytaj@ualberta.ca). A small and a large lake in both M and GL landforms were cored (Table 1). In the case of the GF landform, we found no organic lake sediment in the sandy main basin of large GF-210 (<0.5% organic matter), so instead cored medium-sized GF-60 (Fig. 1, Table 1). Sub-bottom profiles of M-43 and GL-171 indicate steep sides and flat bottoms; thus we assumed that sediment focusing was not substantial at M and GL lakes. In the case of G-16, the depression slopes are modest to steep, thus sediment focusing cannot be ruled out.

Climate in the western Boreal region is subhumid (i.e., in most years, evaporation exceeds precipitation), and combined with the thick veneer of fine to coarse-grained surficial deposits, complex hydrologic processes can result. For example, runoff from fine-grained hillslopes is typically small (Devito et al. 2005*a*), water from peatlands may move to-

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Table 1. Morphological characteristics of the cored lakes.

Lake No.	Age (years)	Landform (primary; secondary)	A_O (ha)	A_T (ha)	A_T:A_O	Z_W (m)	Z_S (m)	Z_T (m)	Z_T:A_O	E_S (m)	E_B (m)
171	10 545	GL; O[a]	10.9[b]	144.2	13.3	0.2	3.7	3.9	0.4	636.2	632.1
169	6 015	GL; O[a]	350.0[b]	1 199	3.4	0.5	0.9	1.4	0.004	636.2	634.8
43	7 483	M ridges and hummocks; O[c]	1.9[b]	17.4[b]	9.1	0.5	2.0	2.5	1.3	654.0	651.5
98	11 000	M ridges and hummocks; O[c]	400.0	6 400	16	1.8	5.6	7.4	0.02	647.7	640.3
16	3 423	GF ridges[c]	43.5[d]	197	4.5	1.3	6.0	7.3	0.2	645.0	637.7
210	NA	GF hummocks[c]	800.0	232 500	290.6	6.0	0	6.0	0.01	655.5	649.5
60	9 417	GF; meltwater channel[c]	100.0	3 914	39.1	3.9	7.1	11.0	0.1	647.7	636.7

Note: A_O, lake surface area; A_T, catchment area (i.e., topographic watershed); Z_w, water + ice depth at core site; Z_S, depth of core sediment; $Z_T = Z_w + Z_S$, depression depth; E_S, lake surface elevation; $E_B = E_S - Z_T$, base elevation; GL, glaciolacustrine; GF, glaciofluvial; M, moraine; O, organic peatland; NA, not available.

[a]Fenton et al. (2003).
[b]Ferone and Devito (2004).
[c]Paulen et al. (2004).
[d]B. Smerdon, Department of Earth and Atmospheric Sciences, University of Alberta, Tory 121, Edmonton, AB T6G 2E3, unpublished data, bsmerdon@ualberta.ca.

Table 2. Chemical characteristics of the study lakes.

Lake No.	pH	TP (μg·L^{-1})	TN (μg·L^{-1})	Ca^{2+} (mg·L^{-1})	Chl *a* (μg·L^{-1})	Trophic status
171[a]	8.1 (1.1)	310 (138)	4639 (1591)	42.3 (10)	29 (16)	HEu
169[b]	8.2	303	7295	46	154	HEu
43[c]	8.0 (1.0)	216 (63)	4787 (4088)	31 (7.2)	33 (37)	HEu
98[c]	9.1 (1.2)	131 (91)	5892	35 (19)	11 (10)	HEu
60[c]	8.9 (0.9)	213 (188)	1604 (479)	43 (5)	22[d] (3)	HEu
16[c]	9.0 (1.2)	43 (22)	1211 (521)	29 (32.7)	8.3 (3.2)	Eu
210[c]	8.1	54.5	1717	32.7	19.9	Eu

Note: Standard deviations are in parentheses. TP, total phosphorus; TN, total nitrogen; Ca^{2+}, calcium; Chl *a*, chlorophyll *a*; Eu, eutrophic (35 < TP ≤ 100 μg·L^{-1}); HEu, hypereutrophic (TP > 100 μg·L^{-1}). Analyses were performed at the Limnology Lab, University of Alberta (www.biology.ualberta.ca/facilities/limnology).

[a]Average of August samples from 1998 to 2002.
[b]August 2001.
[c]Average of August and October 2002.
[d]October 2002.

wards mineral uplands, and subsurface flows in coarse-grained deposits may originate beyond local topographic divides. As a result, lake hydrologic regimes vary with surficial geology, soil type and depth, and elevation (Devito et al. 2005*b*). Precipitation onto and evaporation from the lake surface dominate the water balance of GL-171 (Ferone and Devito 2004); the same is assumed for GL-169. Although GL-171 and GL-169 are located in the regional groundwater recharge zone, seepage rates are extremely low as a result of the low hydraulic conductivity of GL deposits. M deposits in the study area are at higher elevation than GF and GL deposits. Although groundwater recharges at M-43, precipitation onto and evaporation from the lake surface dominate the water balance (Ferone and Devito 2004), with infrequent runoff during wet years (Devito et al. 2005*a*; we assumed the same for M-98 (also called South Twin Lake)). Groundwater discharge is substantial in the case of the GF-lakes, and at GF-16 (Fig. 1), both seepage and spring discharge are important (Smerdon et al. 2005). Persistence of ice-free patches through the period of winter ice cover at GF-M (also informally called Mink) (Fig. 1), and artesian wells in the vicinity of GF-60 that lies in meltwater channel, confirm the importance of groundwater discharge to the GF study lakes (see also Devito et al. 2005*a*).

Typical of Boreal Alberta (D. Walty, Alberta Sustainable Resource Development, Fisheries Management NW, Provincial Building, 9621–96 Avenue, Peace River, AB T8S 1T4, personal communication, Dave.Walty@gov.ab.ca), the study lakes are eutrophic (i.e., TP 35–100 μg·L^{-1}) or hypereutrophic (i.e., TP > 100 μg·L^{-1}) (Table 2). In the study region, lakes began accumulating sediment between 8000 and 3000 years ago (Schweger and Hickman 1989), when summer insolation decreased and humidity increased (Kurtzback and Guetter 1986; Pielou 1991).

Coring and analysis of sediments and soils

Long-term rates of C and sediment accrual were determined by extracting continuous 7.6 cm diameter cores to basal substrate using the vibracoring techniques of Smith (1998). Two long cores per lake were collected, one where water depth was maximum and a second closer to shore, in March 2003. At GL-169, GL-171, and M-43, both overlying water and near-surface sediments were frozen in March to depths of 7, 33, and 50 cm, respectively, and the previously frozen sediment was resampled in July 2003 (see below). Long cores were frozen and cut lengthwise using a band saw, and one-half was archived at the University of Alberta (Edmonton, Alberta). The exposed surface of the thawed

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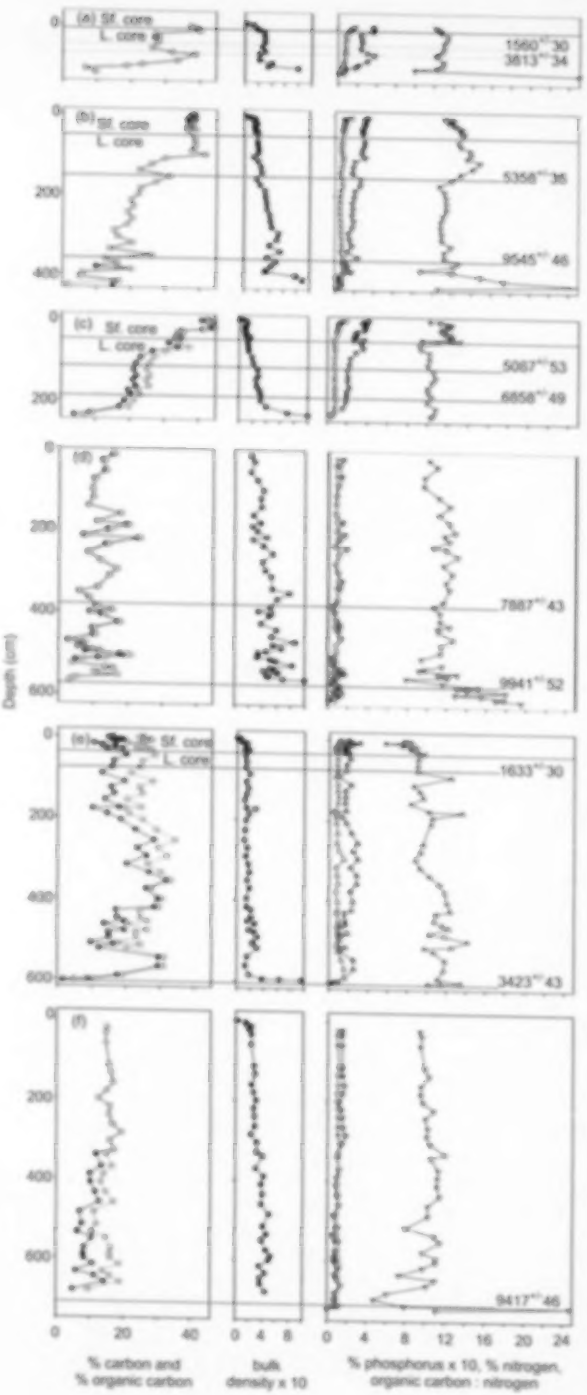

Fig. 2. Left panels: percent total (open circles) and inorganic carbon (solid circles); middle panels: bulk density × 10 (g·mL^{-1}); right panels: % nitrogen content (left-hand open triangles), % phosphorus content × 10 (solid triangles), and organic C:N (right-hand open triangles) for (*a*) GL-169, (*b*) GL-171, (*c*) M-43, (*d*) M-98, (*e*) GF-16, and (*f*) GF-60. Horizontal dashed lines represent dates in radiocarbon years (±SE) before present. L., long core; Sf., surface core.

half was scraped horizontally using a razor blade and described and photographed, then 1 cm^3 subsamples were removed from the center at 5 cm intervals using a 10 mL disposable syringe (tip removed). The remaining undisturbed sediment from the center of the cores was sieved to retrieve macrofossils. Short, 20–30 cm long surface sediment cores were collected in July using a gravity corer fitted with a 5 cm diameter (2 inch) Plexiglas tube and were extruded at 0.5 cm for ^{210}Pb dating and at 2 cm intervals for chemical analysis. Sediment was placed in polyethylene bags, freeze-dried, reweighed to estimate water content and bulk density (BD), and then ground using mortar and pestle. Total C (TC) and nitrogen (N) content were measured using a Perkin-Elmer CNH analyzer (PerkinElmer Inc., Wellesley, Massachusetts) (as per Stainton et al. 1977). Inorganic C content was assumed equivalent to the amount of C that remained after ignition at 550 °C for 12 h (to burn off organic matter) and was determined for a subset of samples that represented the major stratigraphic facies in each core. Total phosphorus (P) content was measured after digestion of sediment (as per Carter 1993) as orthophosphate (as per Stainton et al. 1977).

Chronology

Long-term chronology was based on ^{14}C dates of one to three plant fragments per core (T. Jull, Accelerator Mass Spectrometry Lab, University of Arizona, Tuscon, AZ 85721, USA, unpublished data; supplementary data Table S1),[2] and long-term accrual rates were derived from a date near the bottom of each core. Recent chronologies were derived from ^{210}Pb depletion rates using the constant rate of supply model and verified by comparison with the ^{137}Cs peak (J. Blais, Department of Biology, University of Ottawa, Ottawa, ON K1N 6N5, Canada; supplementary data Tables S2–S5).[2] Briefly, assuming that both the ^{210}Pb flux from the atmosphere to lakes and from lake water to sediments are constant, sedimentation rates can be derived from the decay of ^{210}Pb content with depth (to some background value that is the result of the decay of ^{226}Ra) plus the cumulative dry weight of sediment (Robbins 1978; Robbins et al. 1978). In the case of ^{137}Cs, large amounts were released into the atmosphere as a result of nuclear device testing that peaked in 1963 then declined. Assuming that ^{137}Cs has a 1 year resident time in the water column, a ^{137}Cs peak in the sediment is assigned a median date of 1964 and mean sedimentation rate is arrived at by dividing the cumulative weight of sediments by the number of years since 1964.

[2] Supplementary data for this article are available on our Web site (http://cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 4072. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

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Fig. 3. (*a*) Depression depth (Z_T) at the core site versus long-term total (open circles) and organic (solid circles) C accrual rate (regression line is for all the data). (*b*) Catchment area:lake surface area (A_T:A_O) versus long-term total and organic C accrual rate for GL-169, GL-171, M-43, M-98, GF-16, and GF-60.

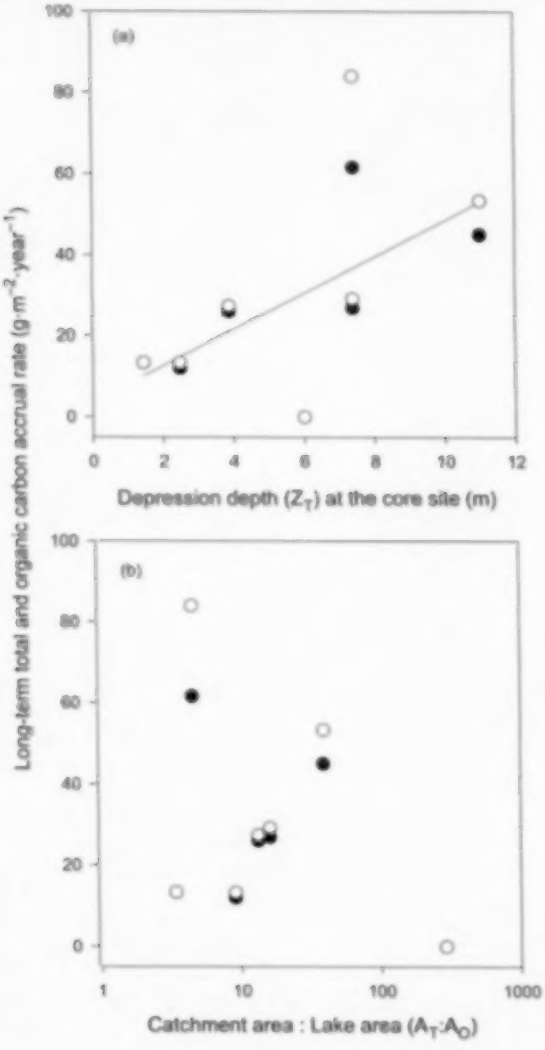
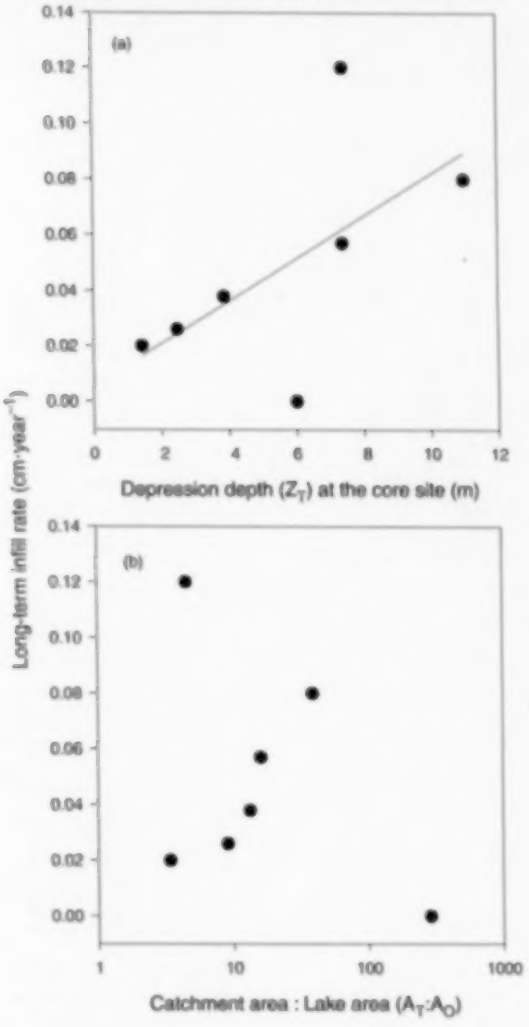

(a)
Long-term total and organic carbon accrual rate (g·m⁻²·year⁻¹)
Depression depth (Z_T) at the core site (m)
(b)
Catchment area : Lake area (A_T:A_O)

Fig. 4. (*a*) Depression depth (Z_T) at the core site versus long-term rate of infill (regression line is for all the data). (*b*) Catchment area:lake surface area (A_T:A_O) versus long-term rate of infill for GL-169, GL-171, M-43, M-98, GF-16, and GF-60.



C:N of soils and plants

The substantially higher bulk N content of aquatic compared with terrestrial detritus and retention of the source C:N fingerprint of detritus after burial in a subaqueous environment (Meyers 1994; Tyson 1995) make it possible to distinguish with some confidence the relative contribution of algae, aquatic macrophytes, and land plants to the lake sediment C pool. To do this, we compared the OC:N (by weight) of sediments with those of dominant aquatic macrophytes, near-shore terrestrial plants, and adjacent wetland soils. Instead of measuring the C:N of phytoplankton, we adopted the range reported by Hecky et al. (1993) (i.e., 9.7 to 17.1 for algae that are nutrient replete to severely N deficient, respectively). Plant and soil samples were oven-dried at 60 °C, and nutrient content was determined as above.

Statistics

We used linear regression to detect significant ($p < 0.05$) correlations between the content and physical structure in the long cores and also to assess the strength of relations among physical variables and C accrual and infill rates.

Results

Core depth and lithology

Among lakes, core depth (Z_{SC}) ranged from about 100 to 700 cm and Z_T from 1.4–11 m (Table 1). Z_{SC} was equivalent to maximum Z_S with two exceptions. In the case of M-43,

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Table 3. Regression statistics and coefficients predicting long-term rates for organic carbon (OC) and total carbon (TC) burial ($g \cdot m^{-2} \cdot year^{-1}$) and infill ($cm \cdot year^{-1}$) from depression depth (Z_T) and catchment area:lake surface area ($A_T:A_O$).

Regression	n	Constant	Z_T coefficient	$A_T:A_O$ coefficient	p	r^2
OC vs. $A_T:A_O$	5	9.58	—	0.934	0.01	0.91
OC vs. Z_T	6	8.23	4.04	—	0.04	0.58
OC vs. Z_T	5	7.87	3.213	—	0.02	0.90
TC vs. $A_T:A_O$	5	8.45	—	1.17	0.004	0.95
TC vs. Z_T	6	7.09	5.31	—	0.04	0.49
TC vs. Z_T	5	6.55	3.997	—	0.01	0.91
Infill vs. $A_T:A_O$	5	0.02	—	0.002	0.01	0.91
Infill vs. Z_T	6	0.01	0.007	—	0.01	0.83
Infill vs. Z_T	5	0.01	0.006	—	<0.001	0.99

Note: GF-210 has been excluded from the analyses, and where $n = 5$, both GF-16 and GF-210 have been excluded.

maximum Z_S was 3.5 and Z_{SC} was 2.2 m or equivalent to mean Z_S. In the case of GF-16, maximum Z_S was 11 m (only a small proportion of the lake lies below the 6 m contour) and Z_{SC} was 7.1 m or close to mean Z_S. Both Z_T and Z_S were maximal in GF than in M and GL lakes (Table 1). Major stratigraphic features of the seven cores are shown in supplementary data Fig. S1.[2]

Core nutrient and sediment content

Among lakes, mean TC content (by weight) ranged from 12% to 29% and organic matter content from 24% to 56% (Figs. 2*a*–2*f*). In general, TC and organic matter content was less in the larger lakes than in smaller lakes (large shallow GL-169 was an exception), and nutrient and sediment content increased with increases in Z_T. On average, N content ranged from 1 to 2 $mg \cdot g^{-1}$ and P from 0.07 to 0.1 $mg \cdot g^{-1}$ (Figs. 2*a*–2*f*). On an areal basis, average TC ranged from 6 to 43 $g \cdot cm^{-2}$, N from 0.6 to 3 $g \cdot cm^{-2}$, P from 0.02 to 0.2 $g \cdot cm^{-2}$, and sediment from 24 to 311 $g \cdot cm^{-2}$.

Nutrient content and sediment quality also varied upcore (Figs. 2*a*–2*f*). In each core, increases in BD corresponded with decreases in OC content (r^2 range = 0.54–0.85, $p < 0.001$), increases in N content corresponded with increases in OC content (r^2 range = 0.86–0.99, $p < 0.001$), and in the case of M-43 and GL-171, increases in P content corresponded with increases OC content ($r^2 = 0.74$, $p < 0.01$ and $r^2 = 0.51$, $p < 0.01$, respectively).

Calcite laminae occurred in M-98, GF-16, and GF-60 (supplementary data Fig. S1).[2] In M-98 where inorganic content was 6% of TC, 4–1 cm wide bands of light marl and several 1 mm thick calcite laminae occurred between 4.9 and 5.0 m and 5.2 and 5.4 m, respectively (Fig. 2*d*). In GF-16 where inorganic C content was 25% of TC, marl bands 1–2 mm thick (occasionally 1 cm thick) occurred typically every 15 cm between 3.6 and 6.0 m (Fig. 2*f*). In Gf-60 where inorganic C content was 30% of TC, 4 mm calcite bands occurred every 5–20 cm between 4.7 and 7.1 m (Fig. 2*f*).

Lake age and long-term C burial and infill rates

Lake age ranged between 3500 and 10 000 years and was within the range previously reported for lakes in central Alberta (e.g., Schweger and Hickman 1989); our results show that relatively young and relatively old lakes occurred in each landform (Table 1). In the case of GF and M but not for GL lakes, the larger lake was older. Within all landforms, the older lake occupied the depression with the lowest relative base elevation (E_B), and the younger lake occupied a depression with relatively high E_B (Table 1).

Among the six lakes that contained sediment, long-term burial rate of TC ranged from 13 to 84 $g \cdot m^{-2} \cdot year^{-1}$ (mean, 37 $g \cdot m^{-2} \cdot year^{-1}$), OC from 12 to 62 $g \cdot m^{-2} \cdot year^{-1}$ (mean, 31 $g \cdot m^{-2} \cdot year^{-1}$) (Fig. 3), and infill rate ranged from 0.02 to 0.1 $cm \cdot year^{-1}$ (Fig. 4). Infill and C accrual rates were correlated with Z_T (Table 3) and were highest in GF-16 and GF-60, where Z_T and inorganic C burial were also higher than in the other lakes (Figs. 3, 4). Infill and C accrual rates were not correlated with $A_T:A_O$ when all lakes were considered. The relationship improves substantially when GL lakes are excluded (Table 3) and will be discussed later.

Recent C accumulation and infill rates among the four-lake subset

Over approximately the last 50 years, mean recent C accumulation rates ranged from 48 to 123 $g \cdot m^{-2} \cdot year^{-1}$ and infill rates from 0.1 to 0.3 $cm \cdot year^{-1}$ in the four-lake subset (Figs. 5*a*, 5*b*). In 2001–2002, C burial rate was highest in relatively low elevation GL-171, intermediate in GL-169, and relatively low in M-43 and GF-16 (Fig. 5*a*). In contrast, recent infill rate was highest in GF-16 and lowest in M-43 (Fig. 5*b*). Among the four lakes in the subset, recent C burial was not related to Z_T or to $A_T:A_O$, and infill was not related to Z_T or to $A_T:A_O$.

C:N fingerprint of sediment carbon

The C:N signature of aquatic plants was 12–14, while that of terrestrial plants was 16–26 (Table 4). The C:N of phytoplankton was assumed 8–11, although values >11 may occur when phytoplankton are nutrient deficient (Hecky et al. 1993). The range of OC:N of swamp soil was 16–26 and of bog soil was 44–69, and in both cases, OC:N increased with depth (Table 4).

In GL-169, OC:N was 8 near the base of limnic sediment and 10–12 through the rest of the core (Fig. 2*a*). In GL-171, C:N was 9 near the bottom and 11–15 upcore (Fig. 2*b*).

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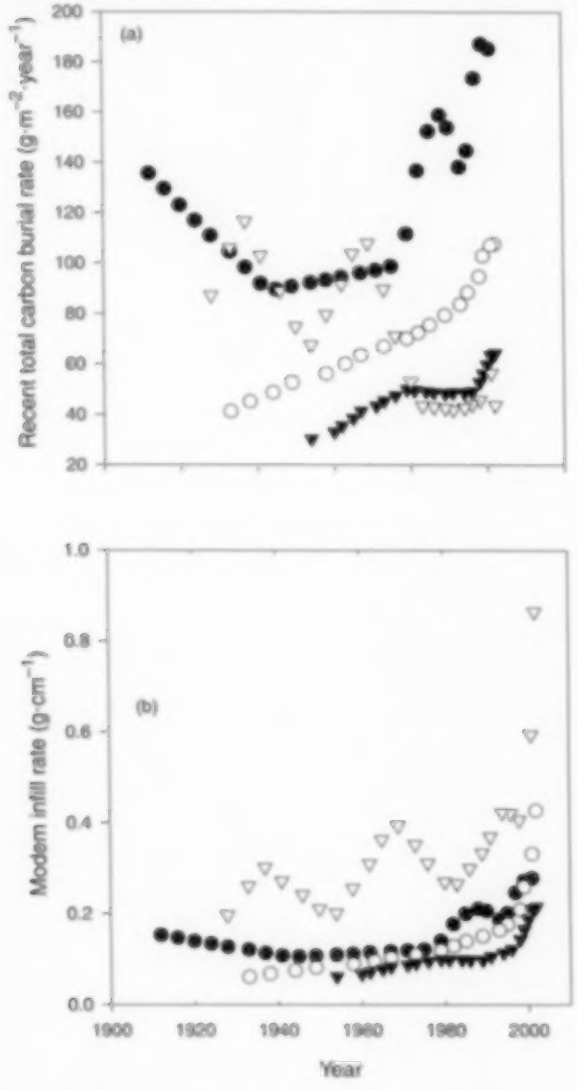

Fig. 5. (*a*) Recent total C accrual rates and (*b*) infill rates over the last 50 years or so in the four-lake subset: GL-169 (open circles), GL-171 (solid circles), M-43 (solid triangles), and GF-16 (open triangles).

Throughout most of the M-43 core, OC:N was 10, but in the top 0.5 m was 9–12 (Fig. 2*c*). In M-98, OC:N was 18 near the core bottom, 10 near the top, and from 11 to 13 midcore (Fig. 2*d*). At GF-16, OC:N decreased upcore from 10 to 12 near the bottom to 10 midcore (but at two intervals was 14) to 8 near the top (Fig. 2*e*). The OC:N at the base of the GF-60 core was 6–12 and 10 upcore (Fig. 2*f*).

Discussion

Landscape factors related to C burial and infill rates

Among the study lakes, Z_S and long-term C accrual and infill rate increased with increases in Z_T. Increases in Z_S did not, however, correspond with increases in lake age. Within each landform, deeper depressions with relatively low E_B started accumulating materials several thousand years earlier and as a result, had greater Z_S than lakes with higher E_B (Table 1). Among landforms, GF-depressions were relatively deep (Table 1) and as a result had the greatest Z_S and long-term C accrual and infill rates (Figs. 3 and 4).

Table 4. Organic carbon (OC):N ratio (by atomic weight) of wetland soils and of submerged aquatics (SAV) and terrestrial plants (TPI) that had colonized lake sediments during a period of drought.

			Wetland soils		
Lake	SAV	TPI	S	B	BLS
GL	13.7[a]	16.5	16.4–26	57.4–69	—
M	11.9[a]	26	16.5	44–68.9	12
GF	13.2	16	—	—	—

Note: S, swamp; B, bog; BLS, lake sediment buried under peat; GL, glaciolacustrine; M, moraine; GF, glaciofluvial. Wetland soils were collected in 2002 by L. Halsey, Axys Environmental Consulting Ltd., 600–555 Fourth Avenue SW, Calgary, AB T2P 3E7, Canada, lhalsey@axys.net.

[a]S. Bayley, Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada, unpublished data, s.bayley@ualberta.ca.

In other landscapes, long-term C accrual rate has been shown to be related to A_T:A_O (Mulholland and Elwood 1982). In deeper, coarse-grained material found in GL landforms, large-scale groundwater flow systems can develop and topographic boundaries may not reflect the area of surface runoff contributions (Devito et al. 2005*b*). As such, a strong relationship using lakes among the three landforms is not expected. GF-60 is located in an outwash channel, and a large portion of the topographic catchment contributes runoff during wet years from M deposits. Lakes with catchment material composed of finer-grained diamicton and lacustrine sediments will have water balances dominated by precipitation and evaporation during most years, but will receive some runoff from portions of the catchment during wetter years (Devito et al. 2005*a*, 2005*b*). C accrual and infill rates increased with increases in A_T:A_O as well as with Z_T in landforms dominated by fine-grained materials. In the case of GF-16, both long-term C burial and infill rates were considerably higher than might be predicted from A_T:A_O or Z_T, and it is known that annual water and nutrient inputs are also relatively high (Smerdon et al. 2005). In the case of GF-210 where organic sediment accrual was negligible, large groundwater inputs are expected, but it is difficult to determine their magnitude (Devito et al. 2005*b*). This data set illustrates the complexity of the Boreal plain landscape and surface and groundwater flows and the need to consider landform features when extrapolating C accrual and dynamics across the landscape.

Recent C accumulation rates in the four-lake subset (range: 48–123 g·m^{-2}·year^{-1}) were not related to trophic status. However, recent mean C burial rates were relatively high in low elevation GL-171 and GL-169 and relatively low in high elevation M-43 and intermediate elevation GF-16. In each of the four lakes, infill rates have increased in recent years but more substantially in GF-16, where rates have doubled since1999, perhaps as a result of commercial excava-

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Table 5. Carbon burial rates in the study lakes compared with published rates for Boreal lakes and wetlands.

Rate (g C·m^{-2}·year^{-1})			
Mean	Range	Lakes and wetlands	Reference
Long-term			
31	0–84	Small Western Boreal Plain lakes	This study
15	—	Albertan lakes	Campbell et al. 2000
	19–24	Eastern Boreal Shield lakes	Molot and Dillon 1996
	25–30	Boreal and Subarctic peatlands	Gorham 1991
50	16–80	Northern peatlands	Gorham et al. 2003
	13–35	Alberta bog	Kuhry and Vitt 1996
31	7–183	Western Boreal fen	Yu et al. 2003
Recent			
80	48–123	Small eutrophic lakes	This study
30	—	Small oligotrophic lakes	Mulholland and Elwood 1982
90	—	Small meso-eutrophic lakes	Mulholland and Elwood 1982
Current			
100	44–185	Small Western Boreal Plain lakes	This study
10	—	Boreal wetlands	Kuhry and Vitt 1996
20	—	Boreal wetlands	Vitt et al. 2000

Note: Long-term rates are derived from a ^{14}C date near the bottom of each core. ^{210}Pb-derived recent rates are averaged over the depth of surface core, and current rates are for 2002.

Table 6. Sediment volume calculated using depression bathymetry (SV_B) compared with sediment volume estimated (SV_E) using combinations of area (A_O), core depth (Z_{SC}), mean sediment depth (Z_{SM}) among the study lakes, and the sediment depth (Z_{SC_A}) and the correction factor (0.667) used in Campbell et al. (2000).

	SV_E ($\times 10^5$ m^3)	
	$= A_O \cdot Z_S$	$= A_O \cdot 0.667 \cdot Z_S$
M-43; $SV_B = 0.71 \times 10^5$ m^3		
$Z_{SC} = 2.0$ m	0.4	0.3
$Z_{SM} = 4.0$ m	**0.8**	0.5
$Z_{SC_A} = 8.0$ m	1.5	1.0
GL-171; $SV_B = 3.58 \times 10^5$ m^3		
$Z_{SC} = 3.7$ m	**4.0**	2.7
$Z_{SM} = 4.0$ m	4.4	2.9
$Z_{SC_A} = 8.0$ m	8.7	5.8
GF-16; $SV_B = 5.29 \times 10^5$ m^3		
$Z_{SC} = 6.4$ m	**6.0**	4.0
$Z_{SM} = 4.0$ m	17.4	11.6
$Z_{SC_A} = 8.0$ m	34.8	23.2

Note: The SV_E closest to SV_B is in bold.

tion of gravel in the vicinity of the lake that may have increased water inflow to the lake (Smerdon et al. 2005).

Comparison of C burial rates with published rates for lakes and wetlands

Among the seven study lakes, long-term mean rate of TC accumulation was 31 g C·m^{-2}·year^{-1} (range: 0–84), which is twice the estimate for Albertan lakes by Campbell et al. (2000) and 20%–30% higher than the estimate for lake sediments in the Eastern Boreal Shield region by Molot and Dillon (1996) (Table 5). High recent TC burial rates in the study lakes are similar to the published C burial rates in small mesoeutrophic lakes (90 g C·m^{-2}·year^{-1}) (Mulholland and Elwood 1982) (Table 5). Higher rates in the study lakes relative to Eastern Boreal Shield lakes may be related to the higher trophic status of Western Boreal Plain lakes as well as the landform complexity of the Western Boreal Plain.

Published mean, long-term C accrual rates in Boreal wetlands range from 31 to 50 g C·m^{-2}·year^{-1} (Table 5) (although the range of rates among individual wetlands is large, i.e., 7–183 g C·m^{-2}·year^{-1}). Published mean recent rates of C burial in wetlands range from 30 to 90 g C·m^{-2}·year^{-1} (Table 5), and although rates among individual wetlands is wide, this indicates that the eutrophic–hypereutrophic study lakes appear to be sequestering C at rates approximate to Boreal wetlands (Table 5).

Estimating the size of the C pool in Boreal lakes

The size of the Boreal lake sediment C pool can be estimated from sediment volume (SV_E), C content, and BD. We assessed how well the general equation (below) used by Campbell et al. (2000) to estimate the OC content of Albertan lakes <10 000 ha worked with our study lakes:

$$(1) \qquad \text{organic C} = Z_S \times \text{org} \times \text{BD} \times 0.667 \times A_O$$

where organic C is in grams, Z_S was assumed 8 m, org is organic C content of sediment and was assumed 0.18 (estimated as 50% of the average organic matter content), BD is bulk density and was assumed 0.14×10^6 g·m^{-3}, 0.667 is the volume-correction factor, and A_O is surface area in m^2. Among the seven study lakes measured, average organic C content was similar to the value assumed in eq.1 by Campbell et al.

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(2000). However, Z_S and BD of the study lakes were one-half and twice the values in eq. 1, respectively. SV_E in eq.1 is calculated as $A_O \times 0.667 \times Z_S$. We estimated SV in this way for the study lakes using the mean Z_S (Z_{SM}) among our lakes as well as Campbell's mean Z_S (Z_{SC_a}) both with and without the correction factor and then compared these estimates with the depression bathymetry-derived sediment volumes (SV_B) for GL-171, M-43, and GF-16 (Table 6). In the case of M-43 and GL-171, the product ($A_O \times 4$ m) matched most closely with SV_B, and in the case of GF-16, the product ($A_O \times Z_{SC_a}$) was the best match. In the extreme case of GF-210, which had no organic sediment, calculated SV_E was greater than SV_B combined from M-43, GL-171, and GL-169. For the case of GL and M but not GF lakes, A_O and a local mean value of Z_S, organic C content, and BD appear to reliably estimate the size of the C pool in small Western Boreal lakes. We conclude that the accuracy of estimates of the rate of C burial and amount of C buried in Boreal small lakes can be improved substantially by considering landscape-level factors, especially surficial geology and local Z_S.

The source of lake sediment C

C:N evidence points to a nutrient-replete phytoplankton C source early in the history of GL-169, GL-171, and M-43 with increasing contributions from macrophytes and (or) land plants as the lakes infilled. In M-98, GF-16, and GF-60 (i.e., the relatively deep depressions), older sediment may be macrophyte and (or) land plant C or alternatively nutrient-deplete phytoplankton, and younger sediment is composed of nutrient-replete phytoplankton. Despite uncertainties, it appears that a large proportion of the organic C buried in Western Boreal Plain lakes is aquatic. This result is consistent with Dean and Gorham's (1998) conclusion that most of the C in the world's lakes is indeed aquatic; however, this disagrees with the conclusions of Mulholland and Elwood (1982) and Molot and Dillon (1996) that Boreal lake sediment C is primarily terrestrial. Molot and Dillon (1996) studied lakes in the Eastern Boreal Shield region that lie on slow-weathering crystalline bedrock and as result have low nutrient content and productivity (Schindler 1978). Also, precipitation exceeds evaporation and as a result stream inflow and outflow dominate lake water budgets in the Eastern Boreal Shield region (Winter and Woo 1990), and as a consequence, terrestrial inputs may be more substantial than in Western Boreal Plain lakes. For the case of Western Boreal Plain lakes, runoff contributions are typically small (Devito et al. 2005*b*) and easily weathered P-rich glacial deposits result in high nutrient content and productivity (e.g., Bayley and Prather 2003).

We conclude that landscape-level factors (especially surficial geology, elevation, depression depth, and A_T:A_O) and lake hydrologic regimes can facilitate linking local-scale data on C burial rates with global aggregate values for the purpose of understanding the global carbon cycle.

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Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats

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Abstract: Bottom trawling causes widespread disturbance of sediments in shelf seas and can have a negative impact on benthic fauna. We conducted a large-scale assessment of bottom trawl fishing of benthic fauna in different habitats, using a theoretical, size-based model that included habitat features. Species richness was estimated based on a generalized body mass versus species richness relationship. The model was validated by sampling 33 stations subject to a range of trawling intensities in four shallow, soft sediment areas in the North Sea. Both the model and the field data demonstrated that trawling reduced biomass, production, and species richness. The impacts of trawling were greatest in areas with low levels of natural disturbance, while the impact of trawling was small in areas with high rates of natural disturbance. For the North Sea, the model showed that the bottom trawl fleet reduced benthic biomass and production by 56% and 21%, respectively, compared with an unfished situation. Because of the many simplifications and assumptions required to synthesize these data, additional work is required to refine the model and evaluate applicability in other geographic areas. Our model enables managers to understand the consequences of altering the distribution of fishing activities on benthic production and hence on food web processes.

Résumé : Le chalutage de fond cause une perturbation générale des sédiments sur les plates-formes marines et peut avoir un impact négatif sur la faune benthique. Nous avons évalué sur une grande échelle les effets de la pêche au chalut de fond sur la faune benthique dans des habitats différents à l'aide d'un modèle théorique basé sur la taille qui inclut des caractéristiques du milieu. Nous avons estimé la richesse spécifique en nous basant sur une relation entre la masse corporelle généralisée et la richesse spécifique. Le modèle a pu être validé par l'échantillonnage de 33 stations soumises à des intensités diverses de chalutage dans quatre régions à sédiments mous de la mer du Nord. Tant le modèle que les données de terrain montrent que le chalutage réduit la biomasse, la production et la richesse en espèces. L'impact du chalutage est maximal dans les zones à perturbations naturelles peu importantes et faible dans les zones de fortes perturbations naturelles. Dans la mer du Nord, le modèle prédit que la flotte de chalutage de fond réduit la biomasse et la production benthiques respectivement de 56 % et de 21 %, par comparaison aux zones non soumises à la pêche. Puisqu'il a fallu faire de nombreuses simplifications et présuppositions afin de synthétiser ces données, il faudra beaucoup de travail additionnel pour raffiner le modèle et pour vérifier s'il s'applique à d'autres régions géographiques. Notre modèle permet aux gestionnaires de comprendre les conséquences du changement des répartitions des activités de pêche sur la production du benthos et, par conséquent, sur les processus du réseau alimentaire.

[Traduit par la Rédaction]

Introduction

Fisheries research traditionally has been driven by the requirement to manage stocks of the harvested species. However, research in the last two decades has increasingly focused on the environmental effects of fishing on non-target fauna and marine habitats (Hall 1999; Sinclair and Valdimarsson 2003) and on ecosystem-based approaches to management that take account of these impacts (Murawski 2000; Brodziak and Link 2002; Link 2002). The impacts of bottom trawls on the seabed are a particular environmental concern because trawls can modify seabed habitat, disrupt food web processes, and extirpate vulnerable species (e.g., Hall 1999). Most existing knowledge of the direct effects of bottom fishing is based on site-specific and relatively small-scale experimental studies (Collie et al. 2000) and comparisons among

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areas subject to known levels of fishing effort (e.g., Hermsen et al. 2003). However, it is not possible to meaningfully extrapolate these results to the scale of the fishery because (*i*) the results of individual studies usually apply to specific habitat types, while many habitat types are impacted by whole fisheries, (*ii*) the spatial distribution of habitat type and other environmental factors affecting the benthic community is unknown or not mapped throughout the area fished, and (*iii*) information on the spatial and temporal distribution of the fishing impact is inadequate (Jennings et al. 2005). The absence of methods for assessing trawling impacts at the scale of the fishery has impeded the development of ecosystem-based management, and attempts to ameliorate the effects of bottom trawling have thus far focused on small-scale area closures to protect vulnerable habitat (e.g., cold-water coral reefs, Hall-Spencer et al. 2002) rather than on management of the overall impact on benthic biomass, production, or diversity.

In coastal seas, the major sources of seabed disturbance are nearbed currents, wind-induced waves (Hall 1994), and bottom trawling and dredging (Jennings and Kaiser 1998). Fishing vessels that target flatfish, gadoids, scallops, and other benthic animals use beam trawls, otter trawls, and scallop dredges that disturb the seafloor to varying depths (from 2 to 20 cm) and kill a substantial fraction of the benthic fauna in the path of the fishing gear. In a global analysis of the effects of bottom fishing, Collie et al. (2000) found that one trawling pass reduced the mean abundance of animals by up to 55%. As benthic invertebrates form the major food source for many commercially exploited fish species, the effects of trawling on the production of benthic communities are of direct relevance for the management of commercial fish stocks and other ecosystem functions the benthos provide (e.g., Link 2002; Widdicombe et al. 2004).

Communities found in locations with high rates of natural disturbance should have characteristics that provide resilience to additional disturbance, since any vulnerable species are unable to become established in conditions of frequent disturbance. Accordingly, the impact of trawling is expected to be proportionately higher at locations that experience low levels of natural disturbance (e.g., deeper water sites) and lower at locations with high levels of natural disturbance (e.g., areas frequently subject to wave action) (e.g., Jennings and Kaiser 1998; Watling and Norse 1998). Despite the potential significance of natural disturbance in determining benthic community responses to trawling impacts, this relationship remains unquantified.

Analyses based on body size consistently explain the fundamental aspects of community structure at many scales and in many ecosystems (Brown and West 2000; Kerr and Dickie 2001). Body size also determines responses to mortality. Since species with smaller body sizes have higher intrinsic rates of increase and can withstand higher rates of mortality, trawled benthic communities tend to be dominated by smaller individuals and species (Kaiser et al. 2000; Duplisea et al. 2002). Ultimately, reductions in the abundance of larger individuals due to trawling may lead to reductions in local species richness. Thus, if all size classes that contain the adults of a given species are lost, then the species becomes extinct, unless it is supported by recruitment or immigration from elsewhere. The cumulative effect of local species loss will be manifest as regional reductions in species richness. If there are consistent relationships between species number and body size in communities, models of trawling impacts on community size composition could readily be developed to predict the direct effects of fishing on species richness.

Here, we assess for the first time the large-scale impacts of an entire bottom trawl fishery on benthic production, biomass, and species richness in the North Sea. The assessment draws on an existing size-based approach for assessing trawling impacts on benthic communities (Duplisea et al. 2002), with new model development to allow for the effects of habitat parameters on the dynamics of benthic communities and to predict the effects of trawling on species richness. The model estimates benthic biomass, production, and species richness in 9 km^2 cells throughout the main fishing grounds prosecuted by the North Sea beam trawl fleet, based on the frequency of trawling effort recorded from the satellite vessel monitoring system (VMS) and environmental parameters of habitat type (sediment type, depth, shear stress, and chlorophyll *a* content of the sediment). Model outputs are extensively validated with field data. Although the model is parameterized and validated using data from the North Sea, the generality of the size-based model ensures that the approach is likely to be applicable in other shallow shelf seas.

Materials and methods

Model development

State variables in the model were defined on the basis of body size and two faunal groups: soft-bodied macrofauna (SOFT), such as polychaetes, and hard-bodied macrofauna (HARD), such as bivalves and crustaceans. The model contained 32 state variables: 16 SOFT (1.9–500 mg) and 16 HARD (50–60 000 mg). Since the 32 state variables represented only two groups differing in body size, there were only two sets of parameters, and the model was relatively simple in both structure and parameter demands. Growth of the population biomass in each body size and organism type compartment was modelled by modifying the basic Lotka–Volterra competition equations to give the population biomass flux for a compartment:

$$(1)\qquad \frac{dB_i}{dt} = B_i r_i \left(\frac{C_i - B_i - \alpha_{ij} B_j}{C_i} \right) - B_i \mathrm{Mort}_i$$

where i and j are competing groups of organisms, B_i is the biomass of animals in compartment i, r is the specific growth rate, C_i is the carrying capacity for compartment i, B_j is the biomass of competitor j, α_{ij} is the competitive influence of a unit of the competitor j biomass on the carrying capacity of population i, and Mort_i is the mortality rate of compartment i. SOFT and HARD were assumed to be in competition (Wilson 1990). Table 2 in Duplisea et al. (2002) summarizes all parameter values for all size classes of the three faunal groups.

The interaction between habitat type and trawling effects was modelled by including relationships between growth and the environment and between mortality and the environment. We included the effect of (*i*) sediment type on trawling mortality, (*ii*) bed shear stress on population growth rate,

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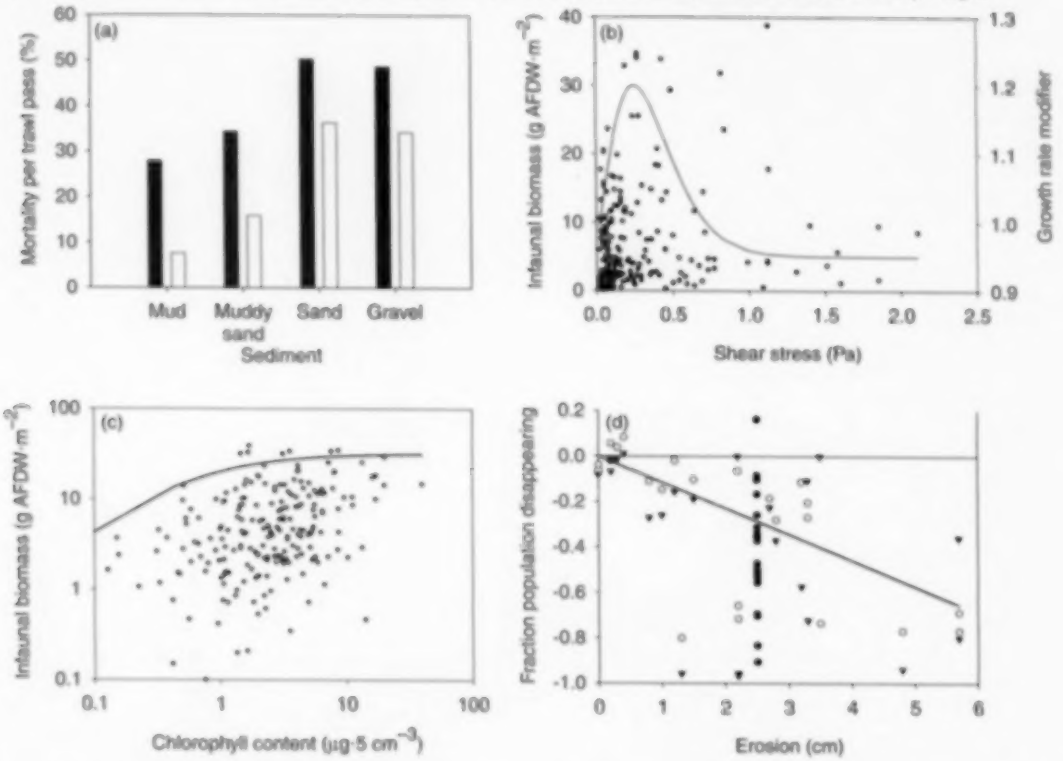
Fig. 1. Parameterization of the model. (*a*) % mortality for a single trawl pass (beam and otter trawl) for hard- (solid) and soft-bodied (open) invertebrates on four sediment categories. (*b*) The relationship between infaunal biomass in the North Sea and bed shear stresses due to the M_2 tide. The plotted line relates shear stress to the growth rate modifier in the model (right axis). (*c*) Infaunal biomass and chlorophyll *a* content of the sediment in the North Sea. See the text for a description of the fitted regression line. (*d*) The fraction of the population of infaunal animals disappearing and sediment erosion. Solid circles, Zühlke and Reise (1994); open circles, hurricane (Yeo and Risk 1979); solid triangles, storm (Yeo and Risk 1979). The regression line was fitted through all data points. AFDW, ash-free dry weight.



(*iii*) chlorophyll *a* content of the sediment on carrying capacity, and (*iv*) sediment erosion on mortality.

Trawling mortality in different sediments

Mortality caused by a single trawl pass on different sediments was estimated from a meta-analysis of experimental studies, including studies carried out in North Sea, by Collie et al. (2000). This is currently the most extensive quantitative database describing the direct effects of trawling on the abundance of benthic species. Only those studies that examined the effects of otter trawling and beam trawling on gravel, mud, muddy sand, and sand habitats in the subtidal zone were included. Because we wanted to estimate the mortality caused by a single trawl pass, we included only those studies that examined the effect of a single trawling event and that sampled the substratum within 10 days of that event. As one trawling event could consist of one or more trawl passes, the effect size was corrected by assuming that the passage of every trawl led to the same proportional reduction. Each species in the database was assigned to the classes SOFT or HARD. The impact of trawling on a species (percent increase or reduction after trawling compared with the condition before trawling or a control area) was $\ln(x + 101) - \ln(101)$ transformed to normalize the data (Collie et al. 2000). The impact of one trawl pass was calculated from the coefficients of a two-way analysis of variance (ANOVA), with sediment type and faunal group as factors. After the analysis, figures were back-transformed to give percent mortality caused by one trawl pass. In total, 381 records from 24 experimental manipulations from 10 studies were used. There was no evidence for body-size-dependent mortality in these data and so no size dependence was assumed. Mortality rates were higher for HARD than for SOFT and were higher for coarser sediments (gravel, sand) than for finer sediments (mud, muddy sand) (Fig. 1*a*). There was a significant effect of sediment ($F_{[3,376]} = 4.9$, $p = 0.0025$) and faunal group ($F_{[1,376]} = 5.4$, $p = 0.0205$) on trawling mortality. Trawling mortality was implemented as a discrete, annual event. This is probably realistic given that most trawling in the North Sea appears to be clustered in time on a small scale. We assumed no direct effect of sediment on benthic growth or on mortality rates (Snelgrove and Butman 1994). Instead we assumed that any correlations between sediment type and benthic community biomass could be explained through the correlation of sediment type with shear stress, chlorophyll *a* content, and erosion rates.

Shear stress

Currents and the associated seabed shear stress can influence food availability for benthic communities (Jenness and

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Duineveld 1985) and benthic secondary production (Warwick and Uncles 1980; Wildish and Peer 1983). High shear stress results in scouring and high current velocities inhibit feeding activity, but some water movement at the seabed is necessary to supply food to the benthos. Below a certain current velocity threshold, food particles transported from other areas may begin to sink to the seabed, where they become available as food to the benthos (Creutzberg 1984). Therefore, we assumed that bottom shear stress affected the biomass of benthic communities primarily through growth rate. A quantile regression showed that infaunal biomass at 209 stations (VLIZ 1986) is limited by M_2 bottom shear stress (generated by the M_2, or semidiurnal, component of the tidal current) according to a second-order polynomial optimum relationship (90th quantile, $p = 0.034$, $R_1 = 0.053$) (for more information on quantile regression, see Cade et al. 1999) (Fig. 1*b*). Visual examination of the relationship among benthic biomass, shear stress, and chlorophyll *a* content of the sediment indicated that there was no interaction between the effect of shear stress and chlorophyll *a* content of the sediment. The relationship between growth rate and shear stress was modelled by multiplying the density-dependent growth rate, as calculated by the Lotka–Volterra equation, with a factor that describes the effect of shear stress on the growth rate. The relationship was modelled as a Gaussian curve according to

$$(2) \qquad G = G_{min} + (G_{max} - G_{min})e^{\frac{(S - S_m)^2}{-V}}$$

where G is the shear-dependent growth rate modifier, G_{min} is the minimal growth rate (0.95), G_{max} is the maximal growth rate (1.2), S is shear stress$^{0.5}$, S_m is the shear stress$^{0.5}$ at which the maximum growth rate is reached (0.5), and V is the variance of the Gaussian curve (0.075).

Carrying capacity

Carrying capacity in the model is simply a scaling factor. Thus, absolute values do not affect the model outcomes, but the relative differences between size classes and stations do. The biomass of benthic communities in a habitat can be limited by the input of food (Beukema and Cadee 1997). The base of the benthic food chain in generally fuelled by microalgae. We used a type II functional response to describe how benthic biomass (g ash-free dry weight·m^{-2}) in the North Sea was limited by the chlorophyll *a* content of the sediment using data from the North Sea Benthos Survey in April–May 1986 (VLIZ 1986) using upper boundary analysis (Blackburn et al. 1992): infaunal biomass = 54.6 chlorophyll *a* / (1 + 1.72 chlorophyll *a*), $R^2 = 0.66$, $F_{[1,12]} = 23.3$, $p = 0.0004$ (Fig. 1*c*).

Sediment erosion due to disturbance by waves and tides

Additional to the normal mortality rates, which relate to body size, sediment movement due to wave action caused by wind and tides can be a major cause of mortality among benthic animals and has been shown to affect secondary production (Emerson 1989). The relationship between sediment erosion and benthos mortality was parameterized using mortality and erosion data from Zühlke and Reise (1994) and Yeo and Risk (1979) and can be described by the following equation: benthos population reduction (%) = 0.14 erosion depth (cm), $R^2 = 0.34$, $n = 67$, $p < 0.0001$ (Fig. 1*d*). SOFT and HARD were assumed to be affected in the same way, as there was no data to justify discriminating between these groups. Yearly mortality rate due to sediment erosion was modelled as erosion mortality = 1 – (1 – mortality per storm)$^{\text{number of storms}}$. A storm was defined as an event where the significant wave height was over 4 m.

Modelled relationships between body mass and species richness

To relate the reduction in biomass of a body mass class to species loss, it was necessary to (*i*) describe the relationship between the number of species in each body mass class and body mass and (*ii*) identify a threshold biomass reduction at which species loss was assumed to occur.

In most taxonomic groups and ecosystems, the relationship between species richness and body size is strongly right-skewed log-normal. Above the modal size class, the relationship between species numbers and body size is generally log-linear (Gaston and Blackburn 2000). The relationship between species richness and body mass was determined from the slope of a regression of the number of species in $\log_3$ body mass classes versus log body mass. All species of free-living infauna and epifauna recorded in the central North Sea by Jennings et al. (2002*b*) were used to determine this relationship, and the heaviest body mass class to which species were assigned was based on their maximum recorded body mass (since maximum observed body mass in trawled areas will fall in response to elevated mortality; for more details see Jennings et al. 2002*b*). Thus, smaller body mass classes had more species than large body mass classes, as they contain both juveniles of large species and adults of small species. The relationship between the log number of species and log body mass for the body mass range considered was linear (Fig. 2*a*, $R^2 = 0.993$, $F_{[1,8]} = 952$, $p < 0.001$). If it is assumed that a species is found in its adult body mass class and in all smaller body mass classes as juveniles, the number of adult species in a body mass class can be described by the slope (derivative) of the relationship describing species number versus body mass (number of adult species per $\log_3$ body mass = 65 exp(–0.35 $\log_3$ body mass)). The relationship between size and species richness that is determined here is valid for soft-sediment communities in the North Sea, and the exact shape of the relationship may differ for other areas and habitats.

The average ratio of size at maturity to maximum body size is two-thirds of body length for species in which growth is described by a Von Bertalanffy growth equation (Charnov and Berrigan 1990). Assuming that body mass increases linearly with the cube of length, the predicted body mass at maturity is 30% of maximum body mass, and almost all mature individuals of a species will be found in the top $\log_3$ body mass class of its size distribution. Adult individuals of each species were assumed to be present only in the heaviest $\log_3$ body mass class. To test the validity of this assumption, we estimated the empirical ratio of the body mass at maturity (W_{mat}) to the maximum body mass (W_{max}) as reported in published literature. If length rather than body mass was reported, we assumed that body mass scaled to length cubed (Charnov 1993).

Species were assumed to be extirpated if the adult biomass fell by 95% from unimpacted levels. This assumption

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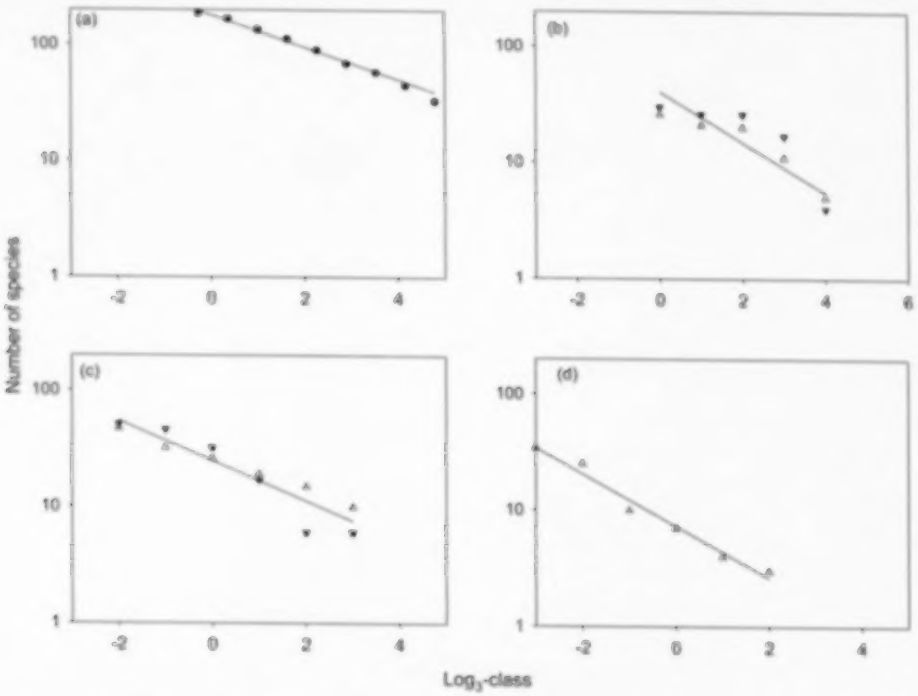
Fig. 2. The number of species per $\log_3$ body mass class in the North Sea. (*a*) Central North Sea, data from Jennings et al. (2002*b*). (*b*) Epifauna sampled with a 2 m beam trawl. (*c*) Large infauna sampled with a toothed dredge. (*d*) Small infauna sampled with a Hamon grab. Lines are least squares regression lines through all data points. Open triangles, Dogger Bank (DB); solid triangles, Northwest Rough (NW).



follows from the World Conservation Union (IUCN) criterion (A1) that a species is critically endangered when adult abundance declines by 90% over 10 years or three generations (Hilton-Taylor 2000). The average, unimpacted biomass per $\log_3$ body mass class was obtained by running the model with trawling intensity set to zero for the Dutch and British sectors of the North Sea in the area south of 56°N, as this was the area for which all environmental data were available. The areas inside the coastal 12 nautical mile (1 n.mi. = 1.853 km) zone and the "plaice box" (a gear restriction area to protect juvenile European plaice, *Pleuronectes platessa*) were excluded from the analysis, because no reliable fishing effort data were available for these areas.

In the model, the loss of the adult size classes did not affect the abundance of the smaller size classes. Despite the local extirpation of a species, we assumed that the biomass of the juveniles of those species that were lost could be replaced by juveniles and adults of smaller body size species. This is consistent with the Lotka–Volterra competition equation model formulations.

Habitat data for the North Sea

Data on sediment, depth, shear stress, and chlorophyll *a* content of the sediment were necessary to validate the model and to make large-scale predictions of the effects of trawling on biomass and production in the North Sea. Sediment data were obtained from digital British Geological Survey (BGS) sediment maps for the North Sea (BGS 2002). Because the relationship between sediment and trawling mortality was parameterized for four sediment classes only (gravel, mud, muddy sand, sand), the BGS classification (Wentworth Folk classification in 15 classes) was simplified into these four classes. All sediments with gravel content of more than 5% were classified as gravel. For sediments with less than 5% gravel, a sand:mud ratio of more than 9:1 was classified as sand. Sediments with a sand:mud ratio between 1:1 and 9:1 were classified as muddy sand, and sediments with a sand:mud ratio smaller than 1:1 were classified as mud. Depth was interpolated using inverse distance weighing from a 1 n.mi. resolution data set. A two-dimensional hydrodynamic model of the northwest European shelf, originally developed at the Proudman Oceanographic Laboratory, UK, was used to predict the mean depth M_2 tidal current at a spatial resolution of 1/8° longitude by 1/12° latitude (approximately 8 km). Bed shear stresses due to the M_2 tide were then calculated using a quadratic expression, with bed stress dependent on the predicted maximum ellipse current and an appropriate bed friction coefficient, which we assumed to have a value of 0.0025 (Howarth and Proctor 1992). Sediment erosion rates due to the combined effects of currents and wind-induced waves were modelled as the maximum erosion for a single event (i.e., the maximum erosion depth that occurred over the whole year). They do not take account of bedload transport or modifications to current associated with bedforms (J.N. Aldridge, CEFAS, Lowestoft, NR33 0HT, UK, unpublished data). On average, there are 4.75 major storms of similar magnitude in a year (Centre for Environment Fisheries and Aquaculture Science 2004). The chloro-

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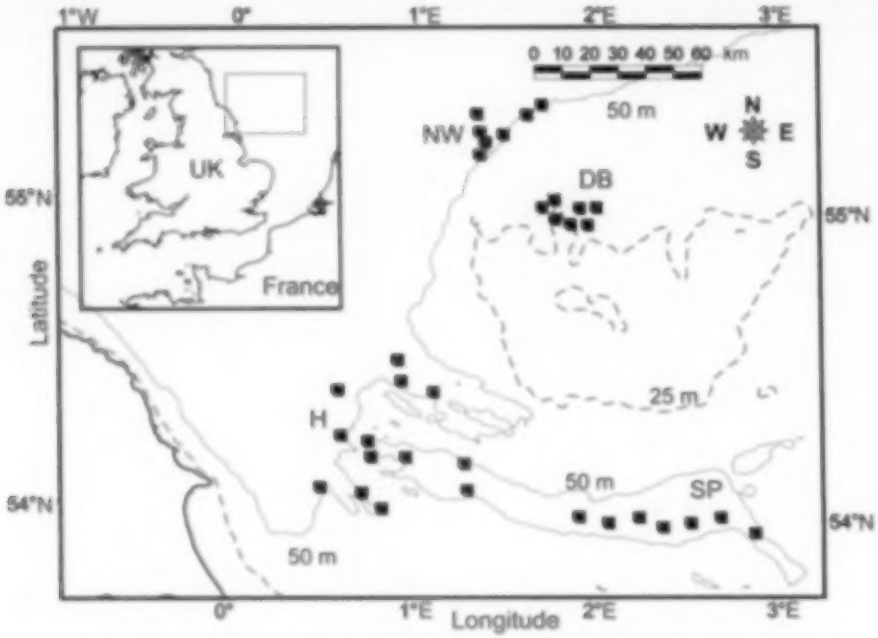
Fig. 3. Overview of the study areas and sampling stations in the North Sea. Stations subject to different levels of trawling disturbance within the four areas: DB, Dogger Bank; H, Hills; NW, Northwest Rough; SP, Silver Pit. The 25 and 50 m depth contours are shown.



phyll *a* content of the sediment was interpolated using inverse distance weighing from the data for 209 stations in the North Sea, which were spaced by 0.5° longitude and latitude (VLIZ 1986).

Trawling effort

Trawling effort was calculated from European Community Satellite Vessel Monitoring System (VMS) data. From 1 January 2000 onwards, all European Community fishing vessels over 24 m were required to report their location, via satellite, to monitoring centres in their flag states, at 2 h intervals. The only exception is made for vessels that undertake trips of <24 h or that fish exclusively within 12 n.mi. of the shoreline (Dann et al. 2002). The proportion of fishing vessels <24 m is probably very low in the offshore areas we examined. The VMS data does not indicate whether a vessel is fishing when it sends position data, but the speed of a vessel can be derived from two consecutive records. Accordingly, vessels travelling at speeds greater than 8 knots and stationary vessels were eliminated as these vessels were assumed not to be fishing (for more details see Dinmore et al. 2003). As the composition of the benthic community is determined by the trawling history, the number of trawl passes per nine square kilometre cell per year was calculated from the number of records in a cell in the period from 1 July 2000 to 31 December 2002. For the calculation of trawling intensity ($year^{-1}$), it was assumed that trawlers fished at a speed of 5 knots, with a total fishing gear width of 24 m (i.e., two beam trawls each of 12 m wide or one 24 m wide otter trawl) (Davidse and De Wilde 2001). Therefore, one record represents a trawled area of 0.449 km^2, and one record in a 9 km^2 cell over the 2.5 year period therefore represents a trawling intensity of 0.0198 $year^{-1}$. The lower limit to the scale at which trawling effort could be evaluated was defined by the resolution of the VMS records. The 9 km^2 scale as used is close to the 1 × 1 n.mi. scale at which fishing effort becomes random (Rijnsdorp et al. 1998). For the Dutch beam-trawling fleet, VMS records were not available for all vessels. Therefore, effort distribution as recorded by the VMS system was corrected to represent total trawling effort as recorded in logbooks by fishers. Additional trawling intensity figures were obtained from records of vessel sightings by fishery protection aircraft as described by Jennings et al. (2001). Within each area, the number of fishing beam or otter trawlers were counted and corrected for the number of visits as a measure of trawling intensity.

Effect of trawling on production, biomass, and species richness in different habitats

Empirical assessments of the effects of trawling were based on measurements of biomass, production, and species richness at sites subject to different levels of fishing intensity in up to four areas with different habitat types. These assessments were used to test model predictions. Data for two of these areas (Silver Pit (SP) and Hills (H)) were taken from Jennings et al. (2001, 2002*a*) and reanalyzed and summarized in this paper.

Experimental design

Each area was characterized by strong gradients in trawling intensity across a homogenous habitat (Fig. 3, Table 1). We expected trawling effort to be spatially heterogeneous in areas of relatively homogeneous habitat because trawlers tend to fish along tows that are recorded in their navigation systems and are known to be free of obstructions that could damage the trawl gear (Auster and Langton 1999; Holland

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Table 1. Environmental and sampling characteristics of the sampled areas in the North Sea.

(*a*) Environmental characterisitics.

	Dogger Bank	Hills	Northwest Rough	Silver Pit
Sediment	Sand	Sand	Sand	Muddy sand
Depth (m)	25–30 (27.3±2.0)	39–62 (51.4±5.3)	49–63 (53.1±5.2)	54–73 (65.3±7.0)
Bed shear stress (Pa)	0.11–0.17 (0.14±0.02)	0.37–0.76 (0.54±0.12)	0.10–0.15 (0.13±0.02)	0.18–0.30 (0.23±0.04)
Erosion (cm)	0.04–0.07 (0.05±0.01)	0.12–0.21 (0.16±0.03)	0.07–0.09 (0.08±0.01)	0.04–0.09 (0.06±0.02)
Chl *a* in sediment ($\mu g \cdot 5\ cm^{-3}$)	4.9–5.6 (5.4±0.3)	2.5–5.0 (3.6±0.8)	3.7–4.3 (4.0±0.3)	2.9–6.4 (4.2±1.2)
Trawling intensity ($year^{-1}$)	0.20–4.88 (1.45±1.97)	0.06–2.35 (0.67±0.72)	0.05–8.17 (2.46±2.90)	0.53–5.38 (1.94±1.80)

(*b*) Sampling characteristics per sampling gear.

	Dogger Bank		Hills		Northwest Rough		Silver Pit	
	Stations × samples	Sampling date	Stations × samples	Sampling date	Stations × samples	Sampling date	Stations × samples	Sampling date
2 m beam trawl	7 × 3	Sept. 2003	13 × 6	Nov. 1999 and May 2000	7 × 3	Mar. 2003	6 × 6	Nov. 1999 and May 2000
Anchor dredge	—	—	13 × 6	Nov. 1999 and May 2000	—	—	6 × 6	Nov. 1999 and May 2000
Toothed dredge	7 × 3	Sept. 2003	—	—	7 × 3	Mar. 2003	—	—
Hamon grab	7 × 5	Sept. 2003	—	—	—	—	—	—
Box corer	—	—	—	—	—	—	24 × 10	Nov. 2000 and Apr. 2001

Note: Data for environmental characterisitics represent range, with mean ± standard deviation in parentheses. Chl *a*, chlorophyll *a*.

and Sutinen 2000). This pattern of effort within habitats persists over many years, and Dinmore et al. (2003) showed that unfished areas are not necessarily unsuitable for trawling. Therefore, at the scale of the study, trawling effort distributions were unlikely to be related to patterns in ecosystem productivity. If fishers nevertheless concentrate in areas with a high ecosystem production, this would decrease the power to detect a negative effect of trawling on benthic production, and therefore our conclusions would be conservative.

Within each area, 7–24 stations were sampled. Areas had the same sediment type (BGS sediment maps) and local environmental conditions, but the stations within areas were subject to different trawling intensities (Table 1). Stations were defined as 6.25 km^2 boxes. The maximum distance between stations within an area varied between 19 and 62 km. Trawling intensities, as calculated from the VMS data, were additionally verified by counting trawl marks on sidescan sonar images of the seabed obtained at the time of sampling (Friedlander et al. 1999).

In the analysis of macrofauna from the SP, station 7 from Jennings et al. (2001, 2002*a*) was excluded because it was situated on the Dutch continental shelf. As a result, effort figures were probably not consistent with data from UK waters. It was also classified as having a different sediment type. VMS fishing effort figures that became available after Jennings et al. (2001, 2002*a*) were included in our analysis, allowing all 24 stations in the UK sector to be used as replicates (conversion of eight stations × three replicates design to 24 stations × one replicate design).

Estimation of trawling disturbance

We used the VMS data to calculate trawling intensity as described earlier. The H and SP were sampled in 1999 prior to the introduction of VMS recording, but it was assumed that patterns in fishing effort were stable over time, thus making it possible to compare the effect of trawling in the different areas on a common trawling intensity scale. There was a significant positive relationship between VMS trawling intensity and the relative trawling intensity calculated from overflight observations for the stations in the SP and H areas at a scale of 3 km × 3 km ($R^2 = 0.72$, $F_{[1,17]} = 45.0$, $p < 0.0001$). This suggests that the trawling effort distribution was reasonably stable through time and that current VMS data could reasonably be used as a surrogate for fishing effort when the SP and H areas were sampled.

Sampling of the invertebrate community

Epifauna were defined as those species that live on the seabed or burrow in it temporarily, while infauna were defined as those for which parts of the body remains more or less permanently in the substratum. Most epifaunal invertebrates are part of the HARD component in the model, while both HARD and SOFT are represented in the infauna. The different components of the benthic community were used as indicators of total benthic community biomass in validation of the model.

We sampled the different components of the benthic community with several sampling devices, partly because of the sediment characteristics in the different areas. Communities of small infaunal invertebrates were sampled with a 0.1 m^2 NIOZ box corer in the SP area and with a 0.1 m^2 Hamon grab in the Dogger Bank (DB) area. Samples were passed through a 1 mm sieve; all animals were picked off the sieve and preserved in 4% buffered formalin. Because the Hamon grab penetrates less deeply into the sediment (<10 cm, often less than 5 cm) than the NIOZ box corer (>20 cm), biomass estimates among gears were not directly comparable. Larger

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infaunal animals were sampled with an anchor dredge (Kaiser et al. 1998) in the SP and H areas and with a toothed dredge in the Northwest Rough (NW) and DB areas. The anchor dredge was towed across the seabed for 1 min. A subsample of 0.2 m^3 of sediment was taken from each anchor dredge sample and sieved through a 1 mm square mesh. All free-living infaunal species retained by the mesh were removed for processing. The toothed dredge had twelve 15 cm long teeth across the 120 cm wide mouth opening and a 5 mm × 5 mm mesh liner and was towed at a speed of 1.5 knots for 3 min. Epifaunal invertebrates were sampled with a 2 m beam trawl fitted with a chain mat and a 2 mm mesh liner (Jennings et al. 1999). The beam trawl was towed at a speed of 1.5 knots for 5 min. All organisms taken in the beam trawl and toothed dredge sample were removed for processing. Start and end positions for the beam trawl and toothed dredge hauls were recorded at DB and NW using the ships' differential global positioning system (DGPS) and the towed distance (m) calculated from these positions. The towing period was timed from the moment that the net contacted the seabed until the moment of hauling. For H and SP, the trawled distance with the beam trawl was not recorded and was assumed to be the average of the distances trawled on DB and NW, which was 300 m. As the same sampling protocol was used in all areas, this assumption may increase the variation in the estimates of biomass per square metre, but not does affect the bias in the estimates. The number of replicate samples, which were taken at haphazard locations within each box, is given in Table 1.

Biomass estimates

All preserved animals from the replicate grabs were sorted and identified to the lowest practicable level in the laboratory, and wet mass was determined after blotting. Animals were identified only in the NW and DB areas. All animals from the replicate beam trawl and dredge samples were identified and individually weighed on heave-compensated balances. Hermit crabs (Paguridae) were weighed after removal from their shells, but animals that secreted their own shells were weighed with the shells intact. Most individuals estimated to weigh less than 0.5 g were preserved and weighed on return to the laboratory. We did not apply shrinkage factors to account for weight changes following preservation, as these were not available for the very wide range of species included in our samples, and blotted weight was recorded in each case (Jennings et al. 2001). Subsequent conversions between wet weight (WW) and ash-free dry weight (AFDW) were made using conversion factors provided by Brey (2001). In the grab and core samples, only infauna with a WW < 1 g were considered in biomass analyses, and only infauna >0.78 mg and <62.5 mg AFDW were considered in production analyses. Animals outside these limits were considered not to have been sampled quantitatively and might have greatly increased the variance in our production estimate. This caused an underestimate of total infaunal production. We only considered epifaunal animals from the beam trawl samples and infaunal animals from the dredge samples

Production estimates

Production was calculated from individual body weights using allometric relationships. For all epifauna and for the infauna sampled with the dredges, we used the production–biomass (*P*:*B*) relationship $\log_{10} P{:}B = -0.233 \log_{10}B - 0.197$ (Jennings et al. 2001). For small infauna sampled with corers–grabs, we used the relationship $\log_{10} P{:}B = -0.236 \times \log_{10}B - 0.431$ (Jennings et al. 2002*a*). Calculated estimates of biomass and production are not identical to those reported by Jennings et al. (2001, 2002*a*) because conversion factors were updated and different selection criteria were used (as described earlier) to make sure that data from all areas were analyzed in the same manner.

Species richness analysis

Loss of diversity was reported as a proportional loss of species from body mass classes >0.2 g. This approach was adopted because the number of local species will be smaller than the number of regional species, and we wanted to apply the model consistently at different scales. In adopting this approach, we assumed that the slope of the regression of the number of species in $\log_3$ body mass classes vs. log body mass was a constant in all communities. We tested this by comparing the slope for the entire central North Sea species pool against the slopes for the sampled (local) communities. We also reported losses of diversity in proportional terms, as none of the sampling methods used to validate model outputs sampled the whole community (as modelled).

The hypothesis that large species decreased at a faster rate than small species with trawling disturbance was tested by comparing the slopes of the regression of species number against trawling intensity (number of species lost per unit trawling effort) for four body mass classes for the three sampling gears used. All species were categorized in one of four $\log_3$ body mass classes (<0.33, 0.33–1, 1–3, and >3 g WW) based on the mass of the largest individual of the species from any station from any of the four sample areas. We only examined species richness in the body mass classes that were considered to be sampled efficiently by the benthic sampling gear and sieves utilized ($\log_3$ body mass classes: grabs, –3 to 2; toothed dredge, –2 to 3; 2 m beam trawl, 0 to 4). No comparisons of species richness across gear types were made because the different areas sampled by the gears did not allow this.

Sediment parameters

A sediment sample was taken for particle-size analysis at each station in the DB and SP areas to check whether significant relationships existed between sediment characteristics and trawling intensity. Sediment samples were wet-sieved through a 500 µm sieve, and the fraction greater than 500 µm was oven-dried at 90 °C for 24 h. This fraction was then dry-sieved at 0.5 phi intervals, down to 1 phi (500 µm) and weighed. The fraction smaller than 500 µm was freeze-dried and analyzed on a Coulter LS 130 laser sizer. The laser sizer results were combined with the dry-sieve results to give the full particle size distribution. As no grabbing or coring could be carried out in the H and NW areas, no sediment data beside BGS sediment maps (BGS 2002) were available for these areas.

Large-scale effects of trawling

The model was used to examine the effect of bottom trawling on benthic productivity in the Dutch and British

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sectors of the North Sea in the area south of 56°N. The areas inside the coastal 12 n.mi. zone and the plaice box were excluded from the analysis, as vessels fishing in these areas are generally not required to record their position through VMS, possibly causing a strong underestimation of trawling intensity in these areas. The whole area was evaluated by calculating biomass and production for each 9 km^2 cell by running the model for 1500 time steps, using the habitat and trawling intensity data described earlier. Biomass and production were compared with a situation without fishing by running the model for the same cells, setting trawling intensity to zero. Total production and biomass was summed over all cells in this area and compared between the normal and no-trawling situation.

Results

Tests of assumptions

We found the W_{mat}/W_{max} ratio for 11 species from 43 populations of bivalves, gastropods, and polychaetes. There was a significant correlation between body mass at maturity and maximum body mass ($n = 43$, $r = 0.87$, $p < 0.001$), with a slope of 0.28. Analysed at the species level, on average the body mass at maturity was 35% of the maximum body mass. (For a table of the W_{mat}/W_{max} ratios, see Supplemental Appendix S1.[2]) The slope of the relationship between species richness and body mass was similar for the central North Sea and the different faunal groups in the two areas that were sampled in this study (Figs. 2*a*–2*d*; ANOVA: group (as in Figs. 2*a*–2*d*), $F_{[1,33]} = 66$, $p < 0.001$; body mass, $F_{[1,33]} = 37$, $p < 0.001$; group × body mass interaction, $F_{[1,33]} = 0.03$, $p = 0.85$).

Model predictions

The model predicted that trawling reduced biomass, production, and species richness of benthic invertebrate communities. The effects of trawling were generally stronger on biomass than on production (Fig. 4). The model predictions showed that the impact of the first passage of a trawl has the greatest effect, while an increase of trawling effort on communities that were already heavily trawled had little additional effect on production or biomass for all habitats. As expected, when shear stresses and erosion rates occur at the optimum value for the growth and survival of the benthos (0.25 Pa and 0 cm, respectively), the modelled production, biomass, and species richness was higher than when values were further away from the optimum (0.75 Pa and 1 cm) (Fig. 4). The model demonstrated that there was an interaction between natural disturbance and fishing disturbance; in situations of high natural disturbance (erosion), biomass, production, and species richness were low irrespective of fishing disturbance. Consequently, additional fishing disturbance had a much smaller effect on the benthos in situations with a high than with a low natural disturbance. At the same level of natural disturbance and trawling intensity, benthic communities on mud and muddy sand were less affected by trawling than those on sand and gravel. Carrying capacity at a particular location changed the amount of biomass supported, but did not change the shape of the response curves.

Biomass, production, and species richness in the North Sea

For the DB and SP areas, there were no significant correlations between the sediment composition parameters and trawling intensity, indicating that local variations in trawling intensity were not influenced by fishers' knowledge of sediment type (Pearson correlations of trawling intensity and mud and sand content by weight, DB: $n = 7$; sand $r = -0.11$, $p = 0.814$; mud $r = -0.02$, $p = 0.974$; SP: $n = 24$; sand $r = -0.30$, $p = 0.16$; mud $r = 0.30$, $p = 0.16$).

Relationships between trawling and benthic community parameters were examined after $\log_{10}$-transformations of biomass, production, and trawling intensity (Figs. 5*a*–5*g*). For epifauna (2 m beam trawl samples), there was a significant negative effect of trawling on biomass and production; for small infauna (box corer and Hamon grab samples), there was a significant negative effect of trawling on biomass (Table 2). We found no effect of trawling on the biomass and production of infauna sampled using the dredges, and we found no significant interactions between the area and trawling intensity for any of the three sampling methods (Table 2). Trawling had a negative impact on species richness for epifauna and grab-sampled infauna, but not for dredge-sampled infauna (Figs. 5*h*–5*i*; Table 2). The initial impact of trawling on biomass, production, and species richness was higher than the additional impact of subsequent trawling events in areas that were already heavily trawled, as indicated by the log-linear relationship among biomass, production, species richness, and trawling intensity.

Validation of model using the field studies

The model was tested by comparing the model predictions of biomass with observed biomass and species richness at the stations that were sampled during the field studies. We used modelled biomasses for the whole community (all faunal groups and all size classes) in all tests. Within areas and sampling gear types, all correlations between the observed biomass in the North Sea and that predicted by the model except one were positive, and 8 out of 12 of these correlations were significant (Table 3). When the observed and predicted values from different areas were combined in one correlation per gear type, all correlations were significantly positive (Table 3). The most extensive data set was for the epifauna sampled with the 2 m beam trawl, with comparable data for all four areas. Accordingly, the relationship between the observed and predicted biomass was highly significant (Table 3; Fig. 6), although the low R^2 indicates that there is a high level of unexplained variation. The original model did not include habitat features (Duplisea et al. 2002) and could not explain the observed variation in biomass of epifauna at this scale (Pearson's correlation coefficient = 0.054, $n = 33$, $p = 0.77$). (A sensitivity analysis of the effect of the parameterization of carrying capacity, trawling mortality, shear-stress-related growth, and erosion-related mortality on the

[2] Supplementary data for this article are available on our Web site (http://cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 4090. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

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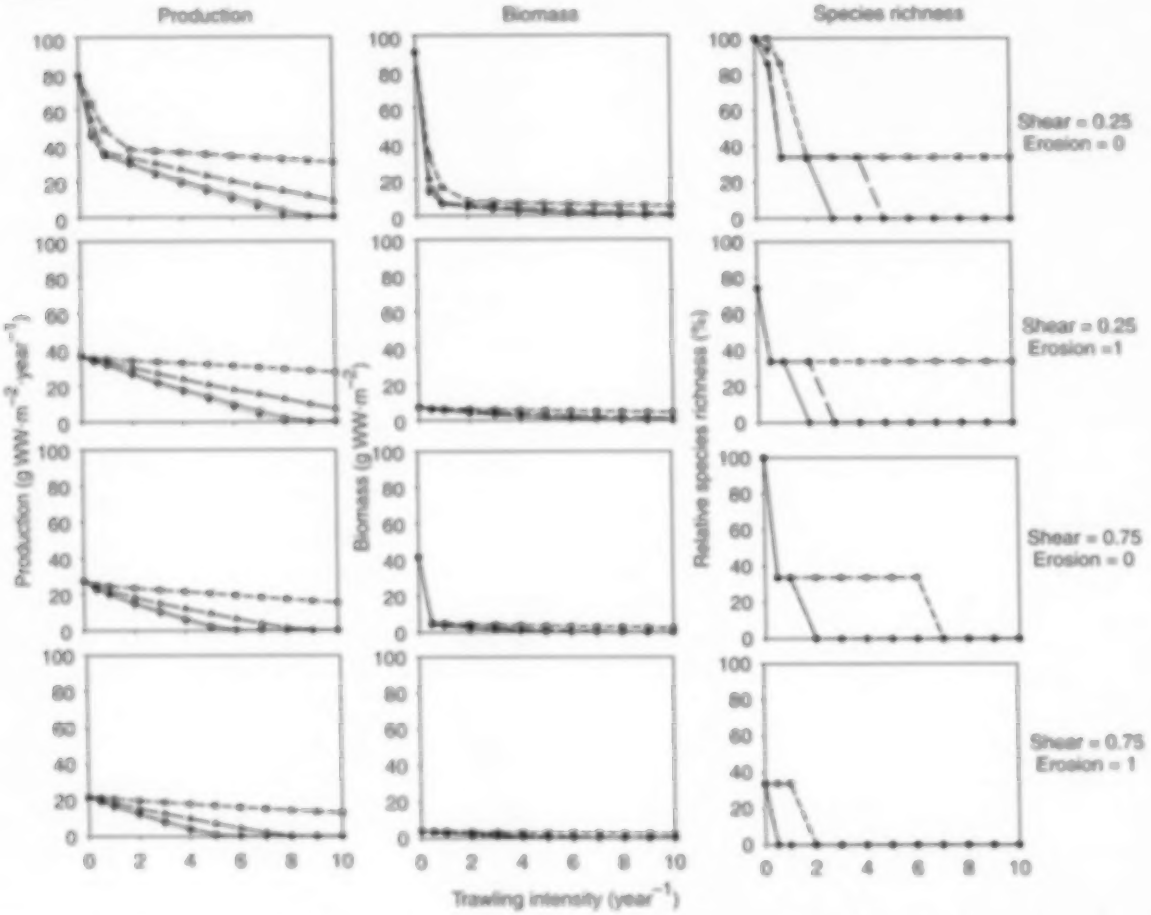
Fig. 4. The relation among trawling intensity, production, biomass, and species richness of benthic communities on four sediment types as calculated by the model. Production, biomass, and relative species richness are given for two levels of shear stress (Pa), two levels of erosion (cm), and four sediment types. Open circle, gravel; solid triangle, sand; open triangle, muddy sand; open square, mud. WW, wet weight.



correlation between observed and modelled biomass is provided in Supplemental Appendix S2.[2])

For species richness within areas, the correlation between observed and modelled species richness was positive for all combinations of areas and sampling gear, although the correlation was never significant (Table 3). Combining the data for the four areas, this correlation was significant for the epifauna sampled with the 2 m beam trawl, but not for the infauna sampled with the grab or the dredge. Species with large body mass disappeared at a faster rate than small species when subjected to trawling (Fig. 7; general linear model with gear type as a categorical factor and body mass class as a continuous variable: gear type, $F_{[2,14]} = 0.79$, $p = 0.47$; body mass class, $F_{[1,14]} = 5.54$, $p = 0.033$; interaction $F_{[2,14]} = 1.13$, $p = 0.35$).

Effect of current trawling levels on biomass and production of benthic communities

According to the model, benthic biomass in the Dutch and UK sector of the North Sea is currently 56% lower than would be expected in the absence of bottom trawling. Benthic production in the Dutch and UK sectors of the North Sea was 21% lower, consistent with a shift in the benthic community towards smaller individuals and species with higher *P*:*B* ratios.

Discussion

This is the first large-scale study of the effect of the interaction between habitat and trawling on benthic biomass, production, and species richness and the first model of the benthic impacts of fishing at the scale of a fishery. Both the model and the field data showed that on shallow, soft sediment habitats, trawling had a large negative effect on biomass and the production of benthic communities in all habitats and that the strength of the impact was linked to the characteristics of the habitat. The initial impact of the first trawl pass was large, while further increasing the trawling intensity in areas where trawling intensity was already high had a smaller additional effect on biomass and production. The model pre-

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Fig. 5. Biomass, production, and species richness of benthic communities in different habitats in the North Sea and trawling intensity with least squares regression lines. (*a*) Biomass for epifauna with 2 m beam trawl, (*b*) biomass for infauna with dredge, (*c*) biomass for infauna with corers–grabs, (*d*) production for epifauna with 2 m beam trawl, (*e*) production for infauna with dredge, (*f*) production for infauna with corers–grabs, (*g*) species richness for epifauna with 2 m beam trawl, (*h*) species richness for large infauna with toothed dredge, (*i*) species richness for small infauna with Hamon grab. Cross and long dash, Dogger Bank; solid triangle and dotted line, Silver Pit; open square and grey line, Northwest Rough; open circle and solid line, Hills. WW, wet weight; AFDW, ash-free dry weight.

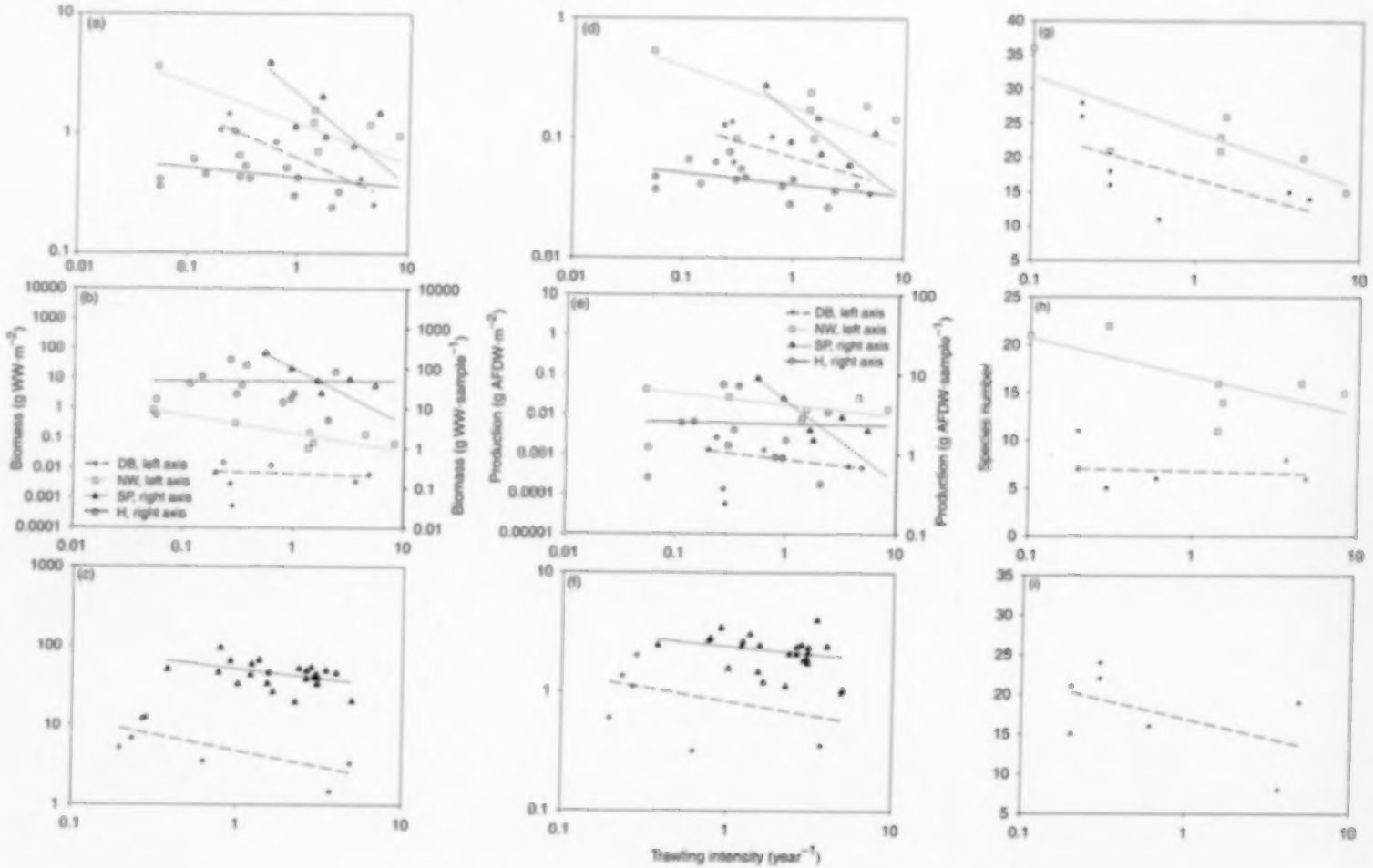

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Table 2. Statistical parameters of the regression relationships among biomass, production, and trawling intensity (all $\log_{10}$-transformed) for four locations and three types of sampling gear for biomass, production, and species richness.

		Area			Trawling intensity			Area × trawling intensity			
	R^2	df	F	p	df	F	p	df	F	p	Residual df
Biomass											
2 m beam trawl	0.72	3	15.5	<0.001	1	14.29	0.0008	3	1.40	0.26	25
Dredges	0.95	3	162.1	<0.001	1	2.32	0.14	3	1.34	0.28	25
Corer–grab	0.87	1	176.0	<0.001	1	18.15	0.002	1	1.28	0.26	27
Production											
2 m beam trawl	0.75	3	20.7	<0.001	1	12.33	0.0017	3	0.80	0.50	25
Dredges	0.94	3	138.9	<0.001	1	0.89	0.35	3	0.44	0.072	25
Corer–grab	0.55	1	29.2	<0.001	1	3.74	0.064	1	0.06	0.80	27
Species richness											
2 m beam trawl	0.60	1	3.53	0.089	1	11.33	0.0071	1	0.10	0.75	10
Dredges	0.83	1	42.8	<0.001	1	2.81	0.12	1	2.76	0.13	10
Corer–grab	0.27	—	—	—	1	1.87	0.23	—	—	—	5

Table 3. Correlation coefficients between observed and modelled biomass and species richness in four areas in the North Sea for three gear categories (Pearson correlation).

Area	2 m beam trawl	Dredges[a]	Box corer – Hamon grab[b]
Biomass			
DB	0.81 (7, 0.027)*	0.14 (7, 0.58)	0.68 (7, 0.095)
NW	0.83 (7, 0.022)*	0.98 (7, <0.001)*	—
SP	0.89 (6, 0.015)*	0.96 (6, 0.002)*	0.30 (24, 0.155)
H	0.36 (13, 0.20)	0.00 (13, 0.99)	—
Combined	0.63 (33, <0.001)*	AD: 0.46 (19, 0.048)*	—
		TD: 0.75 (14, 0.002)*	—
Species richness			
DB	0.737 (7, 0.059)	0.138 (7, 0.767)	0.578 (0.17)
NW	0.692 (7, 0.085)	0.749 (7, 0.053)	—
Combined	0.575 (14, 0.032)*	0.079 (14, 0.78)	—

Note: The n and p values are given in parentheses, respectively. An asterisk (*) indicates significance after step-up false discovery rate correction, an alternative to Bonferroni corrections (Garcia 2004), with a family-wise $p = 0.10$. DB, Dogger Bank; NW, Northwest Rough; SP, Silver Pit; H, Hills; AD, anchor dredge; TD, toothed dredge.

[a]Biomass data included both toothed and anchor dredges; species richness data included only the toothed dredge.

[b]Biomass data included both box corer and Hamon grab; species richness data included only the Hamon grab.

dicted that the biomass of benthic communities in habitats subject to high levels of natural disturbance was less affected by additional trawling disturbance than the community in naturally stable habitats. The effect of trawling was predicted to be smaller on muddy than on sand and gravel sediments, but this effect is relatively unimportant compared with the effect of natural disturbance. In real ecosystems, sediment type and natural disturbance rates are likely to be correlated, with muddy sediments in locations with low natural disturbance and coarser sediments in areas with higher natural disturbance. The field data showed that the least affected area (H) was known to be dynamic in terms of sediment transport and has high levels of erosion and shear stress. The deeper areas NW and SP, which had the lowest erosion rates, were more severely affected by trawling. Large species disappeared at a faster rate in response to trawling than small species, as would be expected given the less resilient life histories of larger animals. This study demonstrates that reductions in species richness in response to chronic trawling disturbance occur primarily because of this loss of large body mass species.

The biomass of infauna and epifauna at 33 stations from four areas in the North Sea were significantly and positively related to the biomass predicted by the model for most of the sampled communities. For epifauna, which were sampled in a comparable way at the largest scale, there was a highly significant correlation between the observed and modelled biomass and the scale of the four areas. The original model (Duplisea et al. 2002), which did not include habitat features, could not explain large-scale patterns in benthic biomass. This shows that habitat interacts with trawling in determining the effects of trawling on benthic communities and that the mechanisms in the model increased our ability to predict the effect of trawling. For infaunal invertebrates, positive

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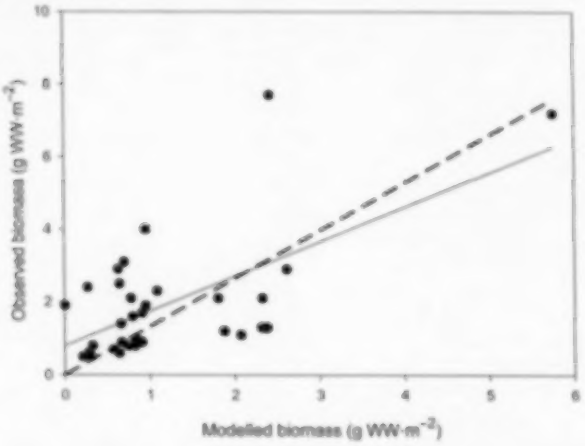
Fig. 6. Modelled community biomass and observed epifaunal biomass. Solid line: least squares regression with both slope and intercept fitted; $R^2 = 0.39$, $F_{[1,31]} = 20.2$, $p < 0.001$. Broken line: intercept removed; $R^2 = 0.29$, $F_{[1,32]} = 75.04$, $p < 0.001$. WW, wet weight.

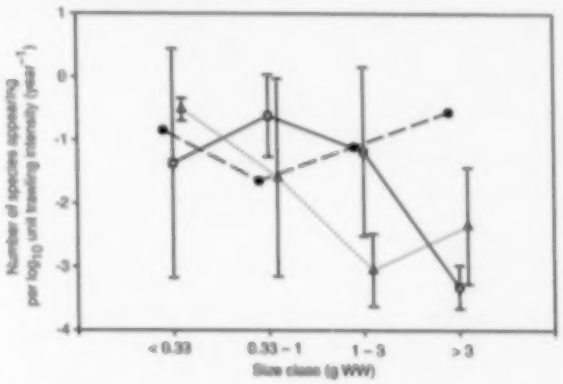


correlations between observed and modelled species richness were not significant, probably because the predicted biomasses were less precise than for epifauna.

These results show that size-based models can be used to predict large-scale patterns in biomass, production, and species richness of benthic invertebrate communities. The model predicted that benthic community biomass was reduced by 56% and production by 21% owing to trawling in the southern North Sea, but this does not imply that 44% of the benthic community is not affected by trawling. This is because the model does not account for shifts in the species composition of communities that are not reflected in simple biomass or production estimates. For example, the intensive exploitation of fish communities often results in species that are more resilient to fishing, thereby replacing those that are not, even though the total abundance may not change (e.g., Dulvy et al. 2000). Large-scale reductions in the production of benthic communities will affect energy flow through the ecosystem. Part of the food otherwise used by the benthic community, predominantly phytoplankton and detritus, might remain unused. This may lead to a greater accumulation of detritus on the sea floor with impacts on microbial communities or the storage of organic matter in sediments or may result in more phytoplankton grazing in the pelagic food chain (Duplisea et al. 2001).

The absolute effects of trawling are smaller in areas with poor growth conditions and high natural disturbance rates because there is less initial biomass. This conclusion is primarily based on the model, which assumes that different benthic groups (soft- and hard-bodied macrofauna) and size classes can only differ in growth and mortality rates. This does not take into account the specific adaptations of species to disturbance. For example, fragile, emergent epifaunal species, like the sea pen (*Virgularia mirabilis*), are likely to be particularly vulnerable to trawling, while species that are tough, flexible, and can easily repair damage, like the starfish (e.g., *Asterias rubens*), may be resilient (Ramsay et al. 2001). If there are species of similar size that differ greatly in vulnerability to trawling, and if resilient species can quickly fill the niche of vulnerable species after trawling, the actual impact of trawling on biomass and production may be smaller than the model predicts. If the species that go extinct occupy unique niches in the ecosystem, which may be common in marine systems (Micheli and Halpern 2005), resources can remain unused after species extinction, thereby reducing community production (Loreau et al. 2002). Extinction of key species may affect other important ecosystem services, such as nutrient cycling and primary production (Lohrer et al. 2004; Solan et al. 2004; Widdicombe et al. 2004). We did not account for such possibilities in our simple model, but further developments could usefully do so if and when adequate data become available to support model development and validation.

Fig. 7. Number of species change (± standard error) per unit trawling intensity for four body mass classes. Solid circle, small infauna; shaded square, large infauna; open triangle: epifauna. WW, wet weight.



Limitations

Because of the many simplifications and assumptions required to synthesize these data, additional work is required to refine the model and evaluate applicability in other geographic areas. The present model does not include predictions for biogenic habitats, like *Modiolus* and *Sabellaria* reefs, where the main habitat features are formed by the animals themselves, with a high diversity of associated species. We would expect substantial trawling effects on production processes and trophic structure in such habitats (Collie et al. 2000), as many of the most vulnerable animals are among those responsible for forming habitat. Indeed, other recent studies have shown that the impact of chronic trawling on production and biomass of benthic communities was severe in biogenic habitats (Bordehore et al. 2003).

The model explained 39% of the observed variation in biomass of epifauna, which indicates that a major part of the variation in biomass in the North Sea remains unexplained. As the fitted intercept of the relationship does not equal zero, the impact of trawling is probably overestimated by the model. However, if the relationship is forced through the origin, the model still explains 29% of observed variation and does not deviate much from the relationship, including an

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intercept. Thus, the model does not capture the real world perfectly, and the modelled values are based on numerous assumptions and relationships that all have a degree of uncertainty. Therefore, we do not know how accurate and precise our estimates of the North Sea-wide impact of trawling on the biomass and production of benthic communities are. The model is also deterministic rather than stochastic and reveals nothing about expected variation in the ecosystem. The sensitivity analysis demonstrated that the correlation of modelled and observed biomass is not particularly sensitive to changes in the parameterization of the model.

North Sea trawl fisheries have a long history, but we only used 2.5 years of recent data for model validation. Given the disproportionate effect of the "first" trawl disturbance, this may explain some of the unexplained variation in the relationship between observed and modelled biomasses. However, the relatively strong correlation between trawling effort as calculated from recent VMS and older, over-flight data showed that effort distribution patterns were relatively stable.

Analyses and modelling of the biomass, production, and species diversity of benthic communities at a large scale is inevitably ambitious, and we had to make many simplifications and generalizations, particularly to parameterize the model to examine large-scale ecological processes. We have to accept these shortcomings if research on large-scale distribution patterns of communities, and in particular on large-scale effects of trawling, in marine ecosystems is to progress at the speed required to support management decision-making. Our model greatly simplifies the structure of the benthic community and ignores recruitment processes that could be limiting at the highest levels of trawling disturbance. However, large infaunal organisms may also play facilitating roles (e.g. Norkko et al. 2002), and in this case, the model will have underestimated the impact of trawling. Instead of compensation for the effect of trawling within the community by small animals, the eradication of large animals will accelerate the loss of smaller animals.

The model assumes that competition is a key mechanism in structuring benthic invertebrate communities. Currently, there is no consensus over the relative importance of competition, predation, and facilitation in marine soft-bottom communities, but competition can play an important role (Branch 1984; Wilson 1990). However, large infaunal organisms may also play important facilitating roles (e.g., Norkko et al. 2002), and in this case, the model will have underestimated the impact of trawling instead of compensating for the effect of trawling within the community, since eradication of large animals will accelerate the loss of smaller animals. However, given the reasonably good fit between observed and predicted biomasses, competition cannot be rejected as a structuring mechanism based on our results.

We deliberately ignored the processes that link the reproductive output of mature individuals to the recruitment of juveniles, which is very poorly known at present. Moreover, migration was ignored. Together, ignoring recruitment and migrations means that recovery from trawling can only occur through local growth of biomass. As a result of this, recovery from trawling is slow, and the model may overestimate the impact of trawling. Therefore, it is important to include these dispersion processes in future developments of the model. The model does not capture seasonal cycles in the recruitment and growth of benthic animals, since growth was treated as continuous. In reality, recruitment of juveniles occurs on a seasonal basis for most species, and growth rates of new biomass are highly dependent upon season in accordance with temperature and primary production. In the real world, one might expect different effects if trawling occurs immediately before adults spawn, compared with later (for example), just after new juveniles have settled. However, as there is no seasonal trend in trawling intensity over the year on a large scale, we expect that this process causes no systematic bias in the effect of trawling as estimated by the model.

Extinction thresholds were set as a proportion of the mean biomass by body mass class in the absence of trawling disturbance. A consequence of this formulation is that species richness can only increase in the areas where the biomass of small animals was depressed below the mean by the dominance of more competitive, large animals. Such instances occurred in areas where natural disturbance was lower than the mean value. Since the empirical data did not show any dome-shaped relationships between trawling and species richness, our assumption does not seem unreasonable. As such, given the constraints of our data, we did not find any evidence to support predictions of the Intermediate Disturbance Hypothesis (Connell 1978), which predicts the highest species richness at intermediate levels of disturbance. Another potential source of bias in this study was that all individuals could not be identified to species. This means that the number of species, particularly in smaller body mass classes, was probably underestimated. This would have resulted in an underestimate of the effect of trawling on species richness.

A further potential critique of our model is that the interaction of habitat and trawling is explained by the inclusions of 10 more habitat parameters, while relatively few data points (33 in four areas) are available for validation. However, most of the model parameters do have an empirical and theoretical basis and were based on empirical observations, thus avoiding one part of the overfitting problem (Ginzburg and Jensen 2004). Almost all relationships between habitat and growth or mortality used in the model were based on empirical data and were significant, even though some had a low R^2 value. Given that four different habitat features plus trawling act simultaneously, it is not surprising that individual habitat features each explain less than 20% of the observed variation. If one factor explained a major part of the variation, hardly any variation would be left that could be explained by other factors.

In conclusion, these results suggest that the use of a size-based model may help to understand the spatial patterns and changes in biomass, production, and species richness in relation to trawling. Overall, our results have shown that trawling affects biomass, production, and species richness of benthic invertebrate communities at a large scale and that the effect of trawling depends on habitat type. Thus, trawling not only reduces fish stocks, but also reduces the abundance of benthic food for commercial fish in a wide range of habitats and hence the carrying capacity of benthivorous species. Therefore, it seems important that fisheries managers consider both the direct and indirect effects of trawling on fish stocks. Given the interaction between habitat and the effect of trawl-

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ing, it may be possible to reduce the impact of trawling on benthic production by redirecting trawling effort from vulnerable to resilient habitats. Moreover, because we observed a nonlinear relationship between trawling and benthic biomass or production, increasing the heterogeneity of fishing effort would also reduce the large-scale impact of trawling. Our new approach for predicting the effects of mortality and environmental factors on species richness is based on the general principles of allometry and a generalized body mass versus species richness relationship, and thus it may be used more widely for predicting spatial patterns of species richness. This model could have practical use for predicting the effects of trawling and natural disturbance on communities. However, as the models are underpinned by the size dependence of vulnerability (i.e., mortality is size dependent), such models could not be applied when vulnerability was determined by size-independent impacts (e.g., pollution).

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Effect of the spatial arrangement of habitat patches on the development of fish habitat models in the littoral zone of a Canadian Shield lake

Anik Brind'Amour and Daniel Boisclair

Abstract: We developed fish habitat models in a Canadian Shield lake using (*i*) a sampling-site approach based on analytical units having a surface area equal to that of sampling sites ($S \sim 200$ m^2), (*ii*) a constant-multiple approach in which the analytical units constituted grouping of adjacent sampling sites in units of increasing sizes (e.g., 2*S* or 3*S*), and (*iii*) a habitat-patch approach in which only contiguous sampling sites with similar environmental characteristics were merged. The best models explaining within-lake variations in fish density, biomass, and community structure on the littoral zone were obtained using the constant-multiple approach, but the predictive power of these models was highly variable ($0 < R^2 < 0.9$) compared with the habitat-patch approach ($0.27 < R^2 < 0.49$). For these approaches, intrinsic variables (estimated inside the analytical units) explained on average 16%–27% of the variations of fish descriptors compared with 6%–32% for extrinsic variables (observed outside analytical units or related to the spatial arrangement of habitat characteristics). Our study suggests that habitat patches are reliable analytical units with which to develop fish-habitat models. Our study also indicates that inclusion of variables that refer to landscape characteristics may significantly improve the predictive power of fish habitat models.

Résumé : Nous avons développé des modèles d'habitats d'un lac du Bouclier canadien en comparant (*i*) une approche dite par sites, dont l'unité d'analyse était équivalente à la dimension des sites d'échantillonnage ($S \sim 200$ m^2), (*ii*) une approche dite contiguë multiple, dont l'unité d'analyse était constituée de groupements de sites de tailles croissantes (p.ex. 2*S* ou 3*S*) et (*iii*) une approche dite de taches d'habitats, dont l'unité d'analyse correspondait à des groupements de sites contigus partageant les mêmes caractéristiques environnementales. Les modèles les plus performants expliquant les variations intra-lac de la densité, de la biomasse et de la structure de la communauté de poissons de la zone littorale ont été obtenus à l'aide des approches par sites ($0 < R^2 < 0{,}9$) et par taches d'habitat ($0{,}27 < R^2 < 0{,}49$). Toutefois, les modèles développés à l'aide de l'approche par sites étaient très variables. Dans les deux approches, les variables propres (variables estimées à l'intérieur d'une unité d'analyse) contribuaient en moyenne entre 16 et 27 % de la variation des descripteurs de la communauté, alors que les variables associées (variables estimées à l'extérieur de l'unité d'analyse ou liées à l'arrangement spatial des habitats) contribuaient entre 6 et 32 %. Notre étude suggère que les taches d'habitat sont des unités d'analyse fiables permettant le développement de modèles d'habitat de poissons. Notre étude indique également que l'inclusion de variables se référant aux caractéristiques du paysage peut améliorer la performance des modèles d'habitat de poissons.

Introduction

Habitat loss is a main threat to the survival of fish species in lakes and rivers (Evans et al. 1996; Richter et al. 1997). For instance, perturbations affecting the littoral zone of lakes have been shown to cause a significant decline in fish productivity (Minns et al. 1996; Brazner and Beals 1997). Perturbations of littoral zones generally involve the replacement of areas of high structural heterogeneity related to the presence of woody debris and macrophytes by areas of lower heterogeneity, such as sandy beaches (Christensen et al. 1996; Radomski and Goeman 2001). Structural heterogeneity often shapes littoral zones in a mosaic of microhabitats suitable for spawning, nesting, foraging, and sheltering (Mittelbach 1981; Werner et al. 1983; Gafny et al. 1992). The presence of habitats that allow fish to perform most activities needed to complete their life cycles may explain the contribution of littoral

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zones to the biological productivity and diversity of lakes (Wetzel 1990; Schiemer and Zalewski 1992). Conservation programs, therefore, call for the development of habitat models that permit the identification of the features of littoral zones that should be protected and the prediction of the effect of perturbations on their fish communities (Brazner and Beals 1997).

Fish habitat models designed for littoral zones generally consist of relationships among fish community descriptors and environmental characteristics defined locally (Bryan and Scarnecchia 1992; Gamboa-Pérez and Schmitter-Soto 1999). However, habitat variation exists over a range of spatial scales (Brind'Amour et al. 2005), and it may be important to identify the size of the units appropriate for testing the existence of relationships among fish and habitat descriptors (Wiens 2002). Dependent and independent variables may be estimated within an area or a volume that corresponds to the sampling sites (*S*; e.g., the area or the volume sampled by a seine or the size of a sampling quadrat). Hence, the size of the units used during the statistical analysis, i.e., the analytical units, may correspond to that of the sampling sites. This approach to the development of habitat models is referred to here as the sampling-site approach. However, there are no indications that the size of the sampling sites, which is determined more by logistical constraints (e.g., the length of a seine, the opening of a trawl, or the time required to survey a volume or surface area) than by ecological considerations, is optimal to model fish habitat quality (Poizat and Pont 1996). This situation may be explored by developing habitat models using analytical units that all constitute the same multiple of the sampling sites (e.g., 2*S* or 3*S*). This approach is further referred to as the constant-multiple approach. Another approach may be to impose a spatial constraint on the procedure such that only contiguous sampling sites with similar environmental characteristics may be merged. This results in analytical units having a size potentially (but not necessarily) different from that of the sampling sites and from that of each other. Because these analytical units have homogeneous environmental characteristics, but attributes different from their surroundings, they are defined as habitat patches (Wiens 1976). The development of habitat models based on the use of such analytical units is hereafter referred to as the habitat-patch approach.

Fish habitat quality at one site may be determined not only by the environmental characteristics found within this site, but also by conditions found in surrounding locations (Lewis et al. 1996; Kocik and Ferreri 1998; Essington and Kitchell 1999). Although the study of the spatial arrangement of sites may contribute to the development of more powerful habitat models, few tests have been performed to assess the effect of the distance between two similar sites or the nature of neighbouring sites on fish habitat quality at a given location (Essington and Kitchell 1999). The objectives of our study were to test (*i*) the effect of the sampling-site, constant-multiple, and habitat-patch approaches on the predictive power of fish habitat models developed for the littoral zone of a lake and (*ii*) the effect of variables that refer to the spatial arrangement of sites on these models.

Materials and methods

Study lake

Sampling was conducted in Lac Drouin (46°14′N, 73°91′W; Lanaudière Region of Québec; Fig. 1). This Canadian Shield lake displays a diversified littoral zone with woody debris, rocky substrate, sandy beaches, and patches of macrophytes of mixed species, e.g., water shield (*Brasenia schreberi*), pipewort (*Eriocaulon aquaticum*), Eurasian water milfoil (*Myriophyllum spicatum*), and water lily (*Nymphea* spp.). It is a mesotrophic lake with a surface area of 31 ha, a maximum depth of 22 m, and a perimeter of 4.8 km. The water column is thermally stratified from May to October. During this period, surface water temperature ranges from 15 °C to 26 °C and bottom temperature ranges from 4 °C to 8 °C. The thermocline forms at 4.5 m deep in mid-June and dissipates in early October.

Sampling procedure

Fish community descriptors and environmental characteristics were quantified over 90 sites covering the complete perimeter of the lake. Fish community descriptors were estimated three times at each site from 29 July to 4 August 2001. All environmental characteristics, with the exceptions of water temperature, dissolved oxygen, macrophyte density, and fetch, were noted at the end of May 2001. Water temperature, dissolved oxygen, and fetch were assessed on each day that fish community descriptors were estimated, and the density of macrophytes was quantified on 29 July 2001. The length of a sampling site was defined by its shore length; the mean length was 53.9 m (SD = 13.2 m). The width of a sampling site was determined by the distance from the shore to the 3 m depth isobath. The limit of 3 m was adopted because it corresponded to the depth at which all fish observed could be correctly counted and identified to the species level while snorkelling. The mean width of a site was 10.5 m (range = 9–12 m). Geographical coordinates were estimated at each site using a global positioning system (GPS 12, Garmin, Salem, Oregon) with a precision of ±10 m. The perimeter of the lake was further separated into two sections comprising 48 (section 1) and 42 (section 2) sites. These sections were surveyed during 2 consecutive days. This sampling procedure was used because a maximum of 50 sites could be surveyed within ~6 h (0900–1500). Based on the sunrise and sunset times, we sampled 4 h after sunrise (~0500) and ended 5.5 h before sunset (~2030). Sampling was limited to this time interval each day because local fish community descriptors may change among periods within a day (dawn, midday, and dusk; Keast and Harker 1977). The sites from two consecutive days (i.e., two sections) were pooled in the same data file to represent the complete perimeter of the lake as a spatial continuum. The data of the three pairs of days that allowed us to obtain three complete perimeters were then added within homologous sites of the lake. This addition of the sections was performed to minimize the effects of daily variations of fish community descriptors at each site. Justification for this procedure is given in Brind'Amour et al. (2005).

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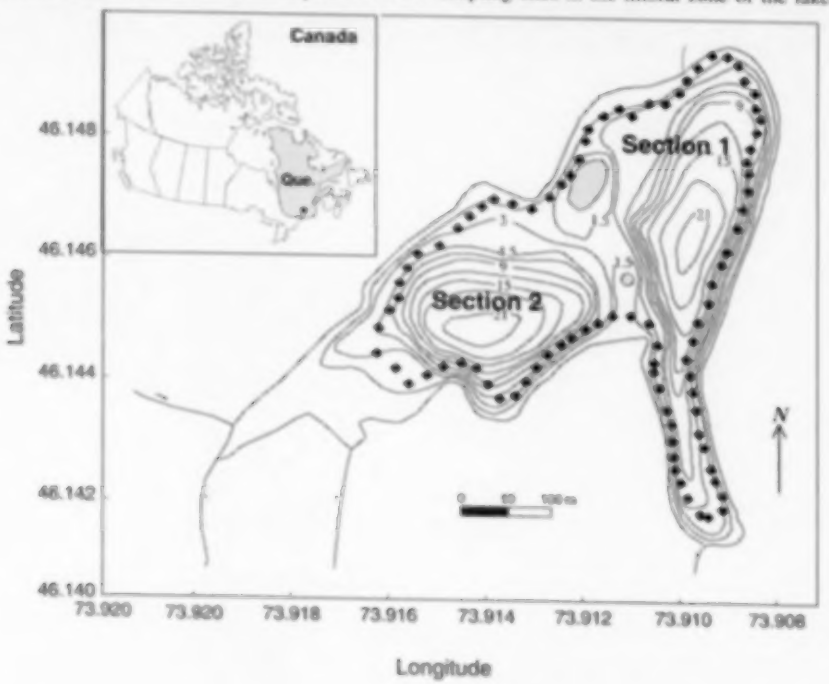
Fig. 1. Map of Lac Drouin, Québec. Solid diamonds represent the 90 sampling sites in the littoral zone of the lake.



Fish community descriptors

Surveys of the fish community were conducted using a modified version of the visual technique described by Harmelin-Vivien et al. (1985). This technique requires two observers to snorkel at the water surface in a zigzag pattern over the complete length and width of a sampling site, following a trajectory globally parallel to the shore. During the surveys, the distance between the two observers was maintained at approximately 4 m. This technique allowed the observers to cover 90% of the total area of each site. The observers maintained a constant swimming speed of approximately 10 m·min^{-1} to minimize fish disturbance and the risk of counting the same individual twice (Eklöv 1997). The snorkellers noted their observations on polyvinyl chloride (PVC) rolls. They identified the species, relative abundance, and approximate size of the fish as they progressed. The relative abundance of fish was categorized according to the following six classes: 1, one individual; 2, two individuals; 3, three individuals; 4, four or five individuals; 5, six to nine individuals; and 6, 10 or more individuals. Each fish was also categorized according to its size. The classification of fish size was based on specific ecological information extracted from Scott and Crossman (1973). This approach, applied to all fish species present in Lac Drouin, resulted in the creation of three size classes: SC_1, shorter than 110 mm total length (TL); SC_2, 110–160 mm TL; SC_3, longer than 160 mm TL. Presampling surveys were conducted in May of the sampling season. During these surveys, all observers swam with a plastic ruler to have a better indication of fish size encountered in the water. Many fish could be seen close (and far) enough to observe their size at different distances from the observer. This operation not only improved the ability of observers to classify fish size consistently, but also minimized the differences among observers. Other details on the visual sampling method may be found in Brind'Amour and Boisclair (2004).

Computations

The fish community at each site was characterized using four descriptors: the total fish density (TFD), the relative fish biomass (RB), the size structure of the fish community, and the fish community composition. Because the abundance data (n_i) obtained during the visual surveys were collected in classes, we transformed them into abundance values as follows: 1, one individual; 2, two individuals; 3, three individuals; 4, five individuals; 5, eight individuals; and 6, 10 individuals. This change of state of the abundance data from discontinuous to continuous variables allowed us to compute the community descriptors. The relative biomass (RB) of fish for any combination of species and size class was estimated as

$$(1) \qquad RB = \Sigma n_{i,s} \times W_{i,s}$$

where $n_{i,s}$ is the number of fish per species per size class and $W_{i,s}$ is the average fish mass (g) per species per size class estimated using the length–mass relationships published in Schneider et al. (2000) and from relationships estimated in our laboratory for Laurentian lakes (Comeau and Boisclair, unpublished data). The size structure of the fish community at each sampling site was described by the percentage of fish belonging in each of the three size classes (SC_1, SC_2, and SC_3).

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Table 1. Intrinsic and extrinsic (Spat) environmental variables that were either sampled or computed at each sampling site for the sampling-site (S), the constant-multiple (C), or the habitat-patch (P) approaches.

Variable	Code	Type	Approaches	Resolution
Average littoral slope (depth (m) on 2 m)	Litt	Intrinsic	S, C, P	Quantitative
Average depth (m)	Z	Intrinsic	S, C, P	Quantitative
Average temperature (°C)	Temp	Intrinsic	S, C, P	Quantitative
Average dissolved oxygen ($mg \cdot L^{-1}$)	O_2	Intrinsic	S, C, P	Quantitative
Substrates				
Sand (<2 mm)	S1	Intrinsic	S, C, P	Presence–absence
Gravel (2–60 mm)	S2	Intrinsic	S, C, P	Presence–absence
Rock (60–250 mm)	S3	Intrinsic	S, C, P	Presence–absence
Boulder (>250 mm)	S4	Intrinsic	S, C, P	Presence–absence
Bedrock	S5	Intrinsic	S, C, P	Presence–absence
Woody debris	S8	Intrinsic	S, C, P	Presence–absence
Macrophytes				
Average density of emergent macrophytes ($stems \cdot m^{-2}$)	Emer	Intrinsic	S, C, P	Quantitative
Average density of submersed macrophytes ($stems \cdot m^{-2}$)	Sub	Intrinsic	S, C, P	Quantitative
Percent cover of *Myriophyllum*	Cov	Intrinsic	S, C, P	Percentage
Presence of pier	Pier	Intrinsic	S, C, P	Presence–absence
Size of the analytical unit (m^2)	Size	Intrinsic	S, C, P	Quantitative
Type of patch	Hab	Intrinsic	P	Nominal
Riparian use				
Cabin/breakwater	U1	Extrinsic	S, C, P	Presence–absence
Forest	U2	Extrinsic	S, C, P	Presence–absence
Beach	U3	Extrinsic	S, C, P	Presence–absence
Bush	U4	Extrinsic	S, C, P	Presence–absence
Riparian slope	Rip	Extrinsic	S, C, P	Nominal
Riparian trees	Tree	Extrinsic	S, C, P	Presence–absence
Fetch (m)	Fet	Extrinsic	S, C, P	Quantitative
Distance to closest tributary (m)	Trib	Extrinsic	S, C, P	Quantitative
Distance to similar patch (m)	Dist	Extrinsic	P	Quantitative
Types of neighbour (left/right)	Neigh-L/R	Extrinsic	P	Nominal

Environmental characteristics

We estimated 16 environmental characteristics at each sampling site (Table 1). Average littoral slope (Litt) was estimated as

$$\text{Litt} = (z_j - z_i) \cdot \Delta d_{j,i}^{-1} \quad (2)$$

where z_i is the depth at one location within a sampling site and $d_{j,i}$ is the difference of the distance between the two locations within the sampling site. Although temperature and dissolved oxygen were measured each day that the fish community was characterized, the averages of temperature and dissolved oxygen were used in the statistical analyses. The density of macrophytes at each site was estimated by two snorkellers in four randomly selected 1 m^2 quadrats (a 1 m^2 frame was thrown from the centre of the sampling site to different directions within each site). The number of stems from emergent and submersed species per 1 m^2 was counted. The average number of stems from the four replicates was used in the statistical analysis. Fetch was defined as the effective distance to the nearer shore in the direction of the predominant wind. Wind data were provided by the meteorological station of the Université de Montréal located at 20 km from Lac Drouin.

Data analysis

Sampling-site approach

Analyses conducted with the sampling-site approach used analytical units identical to those of the sampling sites (Fig. 2*a*). The relationships between the fish community descriptors and the environmental variables were estimated at the scale of individual sampling site.

Constant-multiple approach

The constant-multiple approach consisted of the grouping of adjacent sampling sites (each having a surface area *S*) in units of increasing sizes (e.g., 2*S* or 3*S*; herein referred to as groups of sites; Fig. 2*b*). The analytical units in this approach apply to the groups of contiguous sampling sites. The analytical units could be viewed as a moving window of 1*S*, 2*S*, 3*S*, ..., 6*S* sampling units that shifts forward from any given arbitrary starting point around the lake to make all the possible combinations of merged sites. For instance, an analytical unit equal to 4*S* would have four different combinations of any given sampling site: (1) 1–2–3–4, (2) 2–3–4–5, (3) 3–4–5–6, or (4) 4–5–6–7. We never merged more than six sampling sites (6*S*). This limit was chosen because of statistical constraints. The grouping of six contiguous sampling sites leads to the formation of 15 analytical units of similar sizes. This number of analytical units was the mini-

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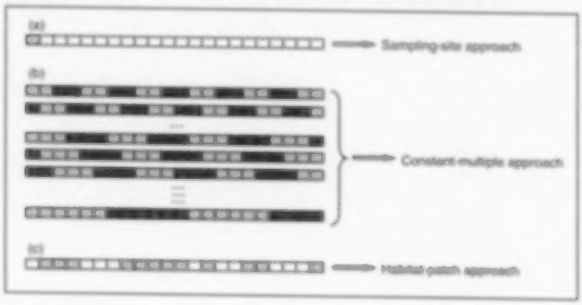
Fig. 2. Schematic description of the three approaches used in this study: (*a*) the sampling-site approach, (*b*) the constant-multiple approach, and (*c*) the habitat-patch approach.



mum sample size that could be used in the statistical analyses, given the number of environmental predictors (Zar 1984). The sums of the values of the fish community descriptors (abundance, biomass, and size classes) were calculated in each analytical unit. Because the grouping of the sampling sites may induce an additive effect, we divided the values of each descriptor by the surface area (i.e., size) of their corresponding analytical unit. Environmental variables were averaged in each analytical unit.

Habitat-patch approach

To verify the effect of habitat patches within the littoral zone, we classified the sampling sites into different types of habitat (Fig. 2*c*). This was performed using two complementary multivariate approaches: clustering and ordination. Although many clustering algorithms are currently offered in statistical packages, we favoured a multilevel hierarchical method. According to Lorr (1983), hierarchical methods are preferable when the variables to cluster are spatially and temporally dynamic. Because some of the environmental data we used were dynamic in space and time (e.g., macrophyte densities and fetch), we chose a hierarchical method. We identified clusters of sites defining different types of habitat using Ward's minimum variance analysis (WCA). Ward's analysis is a hierarchical clustering method that uses an objective function, the sum of squares (SS), the same criterion used in the multivariate analysis of variance. This method attempts to minimize the SS of any two (potential) clusters that can be formed (Legendre and Legendre 1998). Ward's method is based on a squared Euclidean distance, a measure susceptible to the recognized problem of the presence of double zeros (Legendre and Legendre 1998), leading two sites with different species composition to be considered similar simply because they both have no individuals present. Consequently, Ward's method is not recommended with community data, which is commonly composed of large numbers of zero values. In our work, we used Ward's method with environmental data such as littoral slopes, macrophyte densities, and fetch. Because environmental data contains much fewer zero values (29%) than fish community data (41%), the very nature of the kind of data used to apply the Ward's method precluded the problem previously emphasized. Visual confirmation of the clusters defined by WCA was obtained using a principal component analysis (PCA; Legendre and Legendre 1998). We considered that two sites belonged to different habitats if the clusters in which they belonged showed a dissimilarity coefficient ranging from 0.39 to 0.61. This range was chosen based on the visual observation of the dendrogram. Following this procedure, all contiguous sampling sites belonging to the same type of habitat were merged. Values of the fish community descriptors were summed in each habitat patch, and we corrected for additive effect by dividing the descriptor values by the surface area of their corresponding patch. Environmental variables within each patch were also averaged. According to these calculations, five new variables were generated: the type of habitat patch, the size of a habitat patch, the distance (in metres) between two similar habitats, the type of neighbour on the left side of a patch, and the type of neighbour on the right side of a patch.

Intrinsic versus extrinsic environmental variables

We assessed the impact of variables describing the spatial arrangement of analytical units by distinguishing two types of environmental variables: intrinsic and extrinsic (Table 1). We classified the environmental variables that were estimated within an analytical unit as intrinsic. Intrinsic variables included the littoral slope, the average depth, the average temperature, the average dissolved oxygen, the type of substrate, the density of macrophytes, the presence of a pier, and the size of the analytical unit. Extrinsic variables were estimated using conditions found outside the analytical units. These variables included riparian use, fetch, and distance to the closest tributary. However, some extrinsic variables were only estimated using the habitat-patch approach. These variables were type of neighbouring habitat patch (type of neighbour on the left side and type of neighbour on the right side) and the smallest distance to a similar type of patch.

Fish habitat models

We developed empirical models based on the relationships among fish community descriptors and environmental variables at the scale of the sampling sites (sampling-site approach), the scale of a constant number of merged sampling sites (constant-multiple approach), and the scale of the habitat patches (habitat-patch approach). The environmental variables were used as explanatory variables in either multiple regressions, in the case of global metrics (total fish density, relative biomass, and size classes of the fish community), or canonical redundancy analyses (RDA; Rao 1964) computed for the community composition (abundance of species) and transformed using the Hellinger transformation, as proposed by Legendre and Gallagher (2001). The RDA was computed for only two approaches: sampling site and habitat patch. The identification of significant variables was made using either a forward selection of the explanatory variables in SPSS (SPSS 1999) for the global metrics (single response variable) or a forward selection procedure in the program CANOCO (ter Braak and Smilauer 1998) with unrestricted permutations for the community composition (multiple-response variables). Correlation analyses were made prior to the forward selection to diminish the number of environmental variables entering into the forward selection procedure and extract the potential redundancy of the environmental variables. We used a *p*-to-enter level of 0.05 and a *p*-to-

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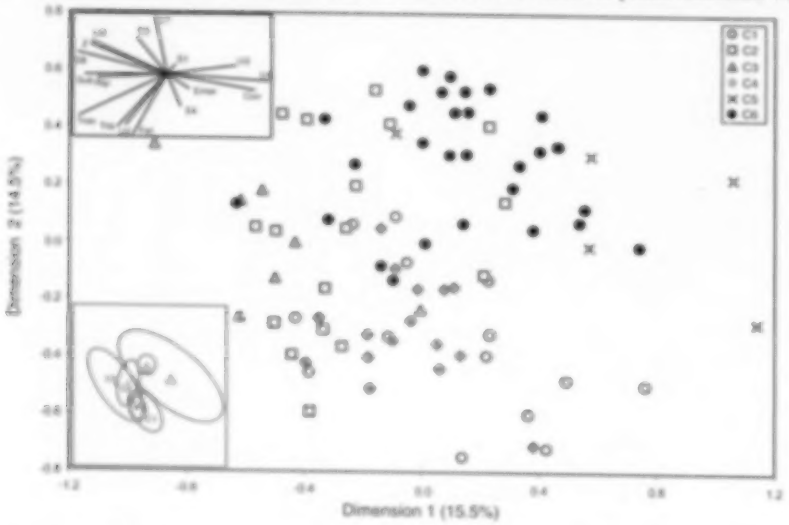
Fig. 3. Site scores on the first and second dimensions (15.5% and 14.5% of variance explained, respectively) for the 90 sites located on the littoral zone of Lac Drouin. The symbols represent the six clusters identified by Ward's cluster analysis. Inset in the upper-left corner: vectors of the environmental variables. Inset in the lower-left corner: contours of the scatter of points associated with each cluster.



remove level of 0.10. Different thresholds were chosen to avoid infinite loops in the selection of variables and to take into consideration the interactions among the variables present in the model. Species present in less than 1% in the survey sites were excluded from all statistical analyses. We computed the R^2 as the fraction of the total variation of the response matrix accounted for by the explanatory data table and corrected it using the adjusted R^2 formula (Zar 1984):

$$\text{(3)} \qquad \text{Adjusted } R^2 = 1 - [(1 - R^2)((n - 1)/(n - m - 1))]$$

where n is the sample size and m is the number of independent explanatory variables.

We conducted an additional step in the development of habitat models using the habitat-patch approach. We verified whether the predictive power obtained in models using patches based on environmental characteristics would be the same if the patches (same numbers and same sizes) were randomly distributed on the littoral zone of the lake. The verification was performed by assessing and comparing the adjusted R^2 obtained at each of the 999 permutations that were performed in the previous analyses (multiple regression analyses and RDA) with the R^2 of the habitat-patch model.

Results

The littoral zone of Lac Drouin showed considerable environmental variability across the sampling sites. The littoral slope (depth (m) on 2 m length) ranged from 0.00 to 1.19 m. The average depth within a sampling site ranged from 0.43 to 2.89 m. Average water temperature in the first 2.5 m depth ranged from 23.8 to 25.1 °C. Average dissolved oxygen in the first 2.5 m depth ranged from 5.98 to 6.64 mg·L^{-1}. Rocks and woody debris were the most common types of substrate, occurring in over 40% of the sampling sites. These substrates were followed by sand and boulders, occurring in nearly 18% of the sites. Bedrock and gravel were the least common types of substrate, occurring less than 1% in the sampling sites. The average density of emergent macrophytes ranged from 0 to 86 stems·m^{-2}, whereas that of submersed macrophytes ranged from 0 to 19 stems·m^{-2}. Nearly 2% of the sites had piers. The most common riparian uses were cabins and breakwaters (62% of the sites). The riparian zone consisted of forested areas in 47% of the sites. Bushes were present in 27% of the sites, and beaches in 6% of the sites. Fetch ranged from 0 to 1406 m. The distance between any given site and the closest tributary ranged from 0 to 1458 m. The average size of the sampling sites was 215 m^2 (range: 105–465 m^2).

Clustering of sampling sites

Grouping of the 90 sampling sites using WCA identified six clusters (Fig. 3). PCA ordinations of the site scores and environmental variables in two dimensions confirmed WCA solutions. The first two dimensions of the PCA of the sampling sites accounted for 15.5% and 14.5% of the variance, respectively. Clusters represented habitat types that differed mostly by their average depth, macrophyte density (emergent or submersed), fetch, and the presence of woody debris and rocky substrates (Table 2). These habitat types were spatially distributed in patches of various sizes, representing a mosaic of habitats along the littoral zone of Lac Drouin (Fig. 4). The size of the patches ranged from 141 to 1175 m^2 but did not differ among habitat types (one-way analysis of variance (ANOVA), $F_{[5,30]} = 1.507$, $p = 0.211$). This suggests that the six habitat types covered the same range of patch sizes. Over 80% of the littoral zone was covered by clusters 6 (C6, 36.1%), 4 (C4, 25.9%), and 2 (C2, 18.6%). The other three clusters (C1, 11.2%; C3, 5.0%; and C5, 3.2%) covered a total of nearly 20% of the littoral zone.

Sampling-site approach

A total of 4293 fish, belonging to eight species, was observed during the study. The species composition of Lake Drouin was characteristic of temperate lake communities

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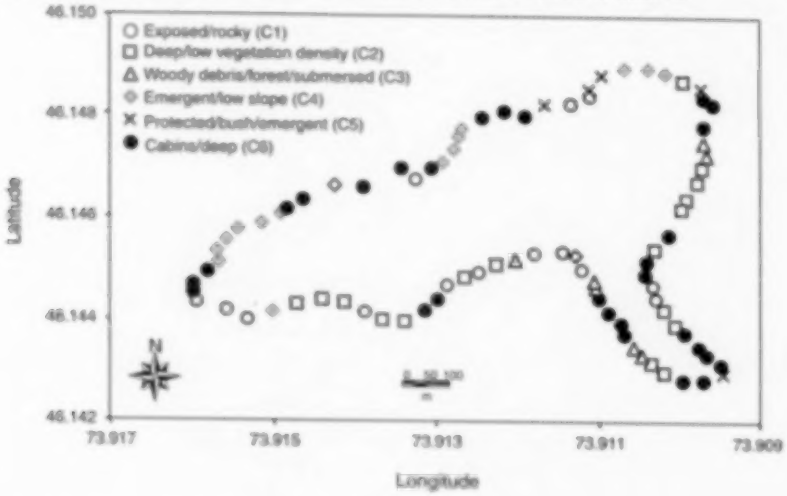
Table 2. Environmental characteristics for each type of habitat display in the littoral zone of Lac Drouin.

Cluster no.	Main designation	Environmental characteristics
1 (C1)	Exposed – rocky substrate	Exposed sites with an average fetch over 600 m where nearly 90% of the sites have boulders as substrate.
2 (C2)	Deep – low macrophyte density	Deep sites with an average over 1.85 m where 100% of the sites have a high riparian slope and are poorly vegetated.
3 (C3)	Woody debris – forest – submersed	Sites with an important littoral slope where 100% of the sites have woody debris as substrate and where the average density of submersed macrophyte reaches 10 stems·m^{-2}.
4 (C4)	Emergent – low slope	Sites with high density of emergent macrophyte (average = 12 stems·m^{-2}), a medium fetch of 350 m, and where 50% of the sites have sand as substrate.
5 (C5)	Protected bush – emergent	Protected sites with an average fetch less than 20 m, with high density of emergent macrophyte (average = 12 stems·m^{-2}), and surrounded by riparian bush.
6 (C6)	Cabins – deep cover	Deep sites (average over 1.85 m), where 90% of the sites have cabins on their riparian zone.

Fig. 4. Spatial structure of the littoral zone of Lac Drouin. Codes for clusters are defined in Table 2.



displaying few or a single dominant species: the pumpkinseed (*Lepomis gibbosus*), which comprised 51% of the fish observed, and six other species representing less than 20% of the observations, including golden shiner (*Notemigonus crysoleucas*), creek chub (*Semotilus atromaculatus*), banded killifish (*Fundulus diaphanus*), brown bullhead (*Ameiurus nebulosus*), yellow perch (*Perca flavescens*), and white sucker (*Catostomus commersoni*). Fathead minnow (*Pimephales promelas*) represented less than 1% of fish observed. However, because the sampling of the fish community was conducted during the day and *A. nebulosus* and *C. commersoni* are known to have limited activity in the nearshore during that period, the two species might have been underrepresented in our study.

The fish community descriptors varied greatly among sampling sites. The TFD ranged from 0.002 to 0.222 fish·m^{-2} (average = 0.078 fish·m^{-2}). Over 50% of the sampling sites had more than 0.065 fish·m^{-2}. The RB ranged from 0.016 to 5.262 g·m^{-2} (average = 0.938 g·m^{-2}), but only 30% of the sites had more than 1 g·m^{-2}. SC_1 comprised 85% of the fish community, whereas SC_2 and SC_3 represented, respectively, ~8% and ~7% of the fish community. SC_1 comprised at least 50% of the fish observed at any sampling site. No fish from SC_2 were observed in 30% of the sampling sites, and these fish represented over 20% of the community in only 10% of the sites. Fish belonging to SC_3 were absent from more than 40% of the sites and represented more than 15% of the fish community in 20% of the sites.

Constant-multiple approach

Average values of the fish community descriptors were generally the same among the groups of analytical units (i.e., 1*S*, 2*S*, ..., 6*S*; Table 3). One exception to this rule was the average TFD that varied between 0.235 fish·m^{-2} for the 1*S* group and 0.133 fish·m^{-2} for the other groups. However, average RB was relatively constant from 1*S* (2.814 g·m^{-2}) to 6*S* (2.690 g·m^{-2}). Similarly, the average percentage of SC_1 (84.56%), SC_2 (8.40%), and SC_3 (7.04%) varied by less than 1% between 1*S* and 6*S*. In contrast with the among-group variability, the within-group variability of the fish community descriptors reached between 5% and 13% (Table 3). The values of the fish community descriptors within groups of analytical units varied between 13- and 300-fold (the RB in the 1*S* unit).

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Table 3. Summary of the variability of the community descriptors found for the constant-multiple approach among the six groupings of sampling sites.

Group	Descriptor	Minimum	Maximum	Mean
1S	TFD	0.002	0.222	0.078
	RB	0.016	5.262	0.937
	SC_1	50.000	100.000	84.560
	SC_2	0.000	35.090	8.390
	SC_3	0.000	34.290	7.040
2S	TFD	0.012	0.101	0.045
	RB	0.079	2.994	0.915
	SC_1	59.783	100.000	84.563
	SC_2	0.000	29.630	8.399
	SC_3	0.000	25.754	7.039
3S	TFD	0.014	0.097	0.045
	RB	0.105	2.375	0.907
	SC_1	62.944	100.000	84.562
	SC_2	0.000	27.566	8.399
	SC_3	0.000	23.650	7.039
4S	TFD	0.017	0.091	0.044
	RB	0.137	2.052	0.899
	SC_1	62.969	100.000	84.759
	SC_2	0.000	24.622	8.281
	SC_3	0.000	21.325	6.960
5S	TFD	0.020	0.082	0.044
	RB	0.204	1.861	0.899
	SC_1	65.158	99.231	84.562
	SC_2	0.000	22.660	8.399
	SC_3	0.000	20.949	7.039
6S	TFD	0.022	0.080	0.044
	RB	0.257	1.921	0.897
	SC_1	68.055	97.826	84.457
	SC_2	1.515	20.550	8.455
	SC_3	0.000	18.075	7.088

Note: TFD, total fish density; RB, relative biomass; SC_1, shorter than 110 mm; SC_2, 110–160 mm; SC_3, longer than 160 mm.

Habitat-patch approach

Habitat patches showed great differences in fish community descriptors. For instance, the values of the TFD showed a 100-fold difference among habitat patches, reaching a maximum of 0.160 fish·m^{-2}, with an average of 0.073 fish·m^{-2}. The RB ranged from 0.020 g·m^{-2} to 2.590 g·m^{-2} (average = 0.823 g·m^{-2}). The percentage of fish belonging to SC_1 varied between 62% and 100%. SC_2 and SC_3 showed similar values, ranging from 0% to 25% and 0% to 23%, respectively.

Fish-habitat models

Sampling-site approach

Fish habitat models developed with the sampling-site approach showed that the TFD and RB correlated with the same environmental variables (Table 4). TFD and RB correlated with the size of the sampling site, fetch, and dissolved oxygen. In addition, TFD was associated with the density of submersed macrophytes. These environmental variables explained 20% (RB) and 31% (TFD) of the variability of fish descriptors. The percent contribution of the three fish size classes to the littoral community was explained by similar environmental variables (Table 4). The fetch (log_{10}), depth, and dissolved oxygen explained a total of 25% of the among-site variability of the percentage of fish that belonged to SC_1. Variation in the percentage of the fish community that belonged to SC_2 was explained by the presence of boulders, the fetch, the presence of woody debris, and the presence of piers. These variables explained a total of 25% of the SC_2 variability. The fetch and the depth explained 19% of SC_3 variability.

Habitat models developed for the whole fish community using the redundancy analysis (RDA) showed that only the first dimension was statistically significant and accounted for 58.1% of the among-site variability of the species composition. The ordination did not show obvious fish assemblages (Fig. 5), but associations among the fish species and the environmental variables could be observed. *Ameiurus nebulosus* and *C. commersoni* were positively associated with the density of emergent macrophytes (log_{10}). The cyprinids (*N. cryseleucas* and *S. atromaculatus*) and *F. diaphanus* were positively associated with the presence of woody debris and depth. *Perca flavescens* was associated with the temperature, whereas *L. gibbosus* showed no clear association with any environmental variable.

The relative contribution of intrinsic environmental variables (16%) was nearly twice as important as the contribution of the variables referring to spatial arrangement (9%) of the analytical unit (Figs. 6*a* and 6*b*). Two exceptions to this rule were the RB and the percentage of SC_1. The importance of intrinsic variables explained in the RB model (7%) were half as important as the extrinsic variables (14%), whereas both types of variables (intrinsic and extrinsic) showed equivalent relative contributions to the SC_1 model (~13%).

Constant-multiple approach

The percentage of variance of the fish descriptors models explained by the environmental variables using the constant-multiple approach varied widely within each group of analytical units (Table 5). For instance, in the 5*S* analytical unit, the R^2 of the RB varied from 0.00 to 0.61. The environmental variables that contributed the most to the models also varied greatly among the groups of analytical units (see details of models in Appendix A). However, certain associations among environmental variables and community descriptors gave consistently better R^2 values. The TFD variability in all the analytical units (1*S* to 6*S*) was best explained when either the size of the analytical unit or the presence of boulders was in the models (R^2 range: 0.31–0.84). The R^2 of the RB models was highest when the density of emergent macrophytes was included in the models (R^2 range: 0.66–0.90). The increase of R^2 in the RB models was particularly obvious in the 4*S* and 6*S* analytical units. The models developed for the percentage of SC_1 showed higher R^2 in broader analytical units (4*S*–6*S*) when the fetch and the presence of boulders were both in the models (R^2 range: 0.44–0.86). In the SC_2 models, the presence of boulders (negative correlation) was the variable contributing most to the R^2 in the 1*S*, 2*S*, and 3*S* analytical units (R^2 range: 0.22–0.44). At broader analytical units (4*S*–6*S*), the presence of beaches, together with the presence boulders (negative correlation), were the variables contribut-

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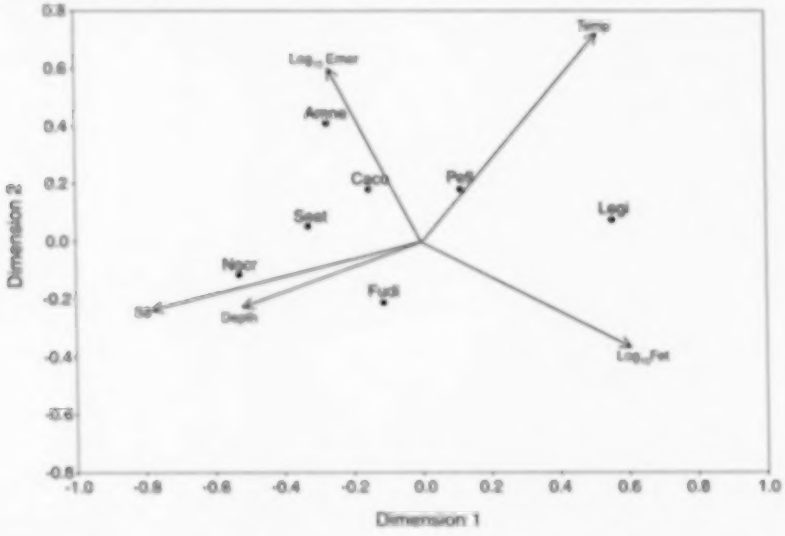
Table 4. Sampling-site models developed for the total fish density (TFD), the relative biomass (RB), the size classes of fish (SC_s) ($n = 90$), and the relative contributions of the intrinsic and extrinsic (spatial) variables.

Equation	Adjusted R^2	Intrinsic	Extrinsic
$TFD = 2.767 - 0.001\ Size - 0.133\ \log_{10}Fet - 0.376\ O_2 + 0.006\ Sub$	0.31***	0.24	0.07
$RB = 53.261 - 0.014\ Size - 1.955\ \log_{10}Fet - 7.628\ O_2$	0.21***	0.07	0.14
$SC_1 = -112.545 + 12.101\ Fet - 5.246\ Depth + 32.787\ O_2$	0.25***	0.13	0.12
$SC_2 = 10.458 - 6.457\ S4 - 5.779\ \log_{10}Fet + 3.854\ S8 - 11.927\ Pier$	0.25***	0.19	0.06
$SC_3 = 0.387 + 5.135\ Depth - 4.482\ \log_{10}Fet$	0.19***	0.15	0.04

Note: Variable codes are defined in Table 1. ***, $p \leq 0.001$.

Fig. 5. Ordination from the redundancy analysis (RDA) showing the relationships among fish species and environmental variables for the habitat-patch model. Only the first dimension of each model was significant and accounted for 58.1% of the fish community variability. Legi, *Lepomis gibbosus*; Nocr, *Notemigonus crysoleucas*; Seat, *Semotilus atromaculatus*; Fudi, *Fundulus diaphanus*; Amne, *Ameiurus nebulosus*; Peca, *Perca flavescens*; Caco, *Catostomus commersoni*; Temp, average temperature; Fet, fetch; S8, woody debris; Emer, average density of emergent macrophytes.



ing the most to the SC_2 models (R^2 range: 0.45–0.89). In almost all the analytical units (1*S*–5*S*), SC_3 variations were explained by models that comprised average depth as an independent variable (R^2 range: 0.19–0.38). In the 6*S* analytical unit, variables related to the riparian use (forest, beach) contributed the most to the models (R^2 range: 0.33–0.65).

Despite the high variability observed within the groups of analytical units, the predictive power of models generally increased as the size of the analytical unit increased (average R^2 values: 1*S*, 0.24; 2*S*, 0.32; 3*S*, 0.40; 4*S*, 0.42; 5*S*, 0.46; 6*S*, 0.58). Significant differences in R^2 were found between the two smaller groups of analytical units (1*S* and 2*S*) and the larger group (6*S*; one-way ANOVA, $F_{[3,99]} = 4.863$, $p < 0.001$).

The relative contribution of the intrinsic environmental variables to the models of the fish community descriptors was relatively stable across the sizes of the analytical units (Fig. 6*a*). However, the relative contribution of the extrinsic variables increased with the size of the analytical units (Fig. 6*b*). The later relationship was particularly strong for the three size classes of fish. Significant positive correlations were found among the relative contribution of extrinsic variables and the size of analytical units (SC_1: Pearson $r = 0.60$, $n = 21$, $p = 0.004$; SC_2, Pearson $r = 0.67$, $n = 21$, $p = 0.001$; SC_3, Pearson $r = 0.50$, $n = 21$, $p = 0.021$).

Habitat-patch approach

Predictive power (R^2) of the models developed using the habitat-patch approach ranged from 0.30 (SC_3) to 0.49 (SC_1) (Table 6). Fetch was an important predictor of the fish community descriptors, explaining 13%–31% of the total variability in every model. The presence of woody debris, the fetch, and the presence of forest on the riparian shore explained 43% of the TFD variability. The model developed for the RB included two variables, fetch and density of submersed macrophytes. Together, these two variables explained 43% of the RB variability. The fetch, the density of submersed macrophytes, and the size of the habitat patch explained 49% of the SC_1 variability. The model developed for the SC_2 included the presence of boulders, the distance to a tributary, and the percent cover of *Myriophyllum*. The three variables explained 44% of the SC_2 variability. Environmen-

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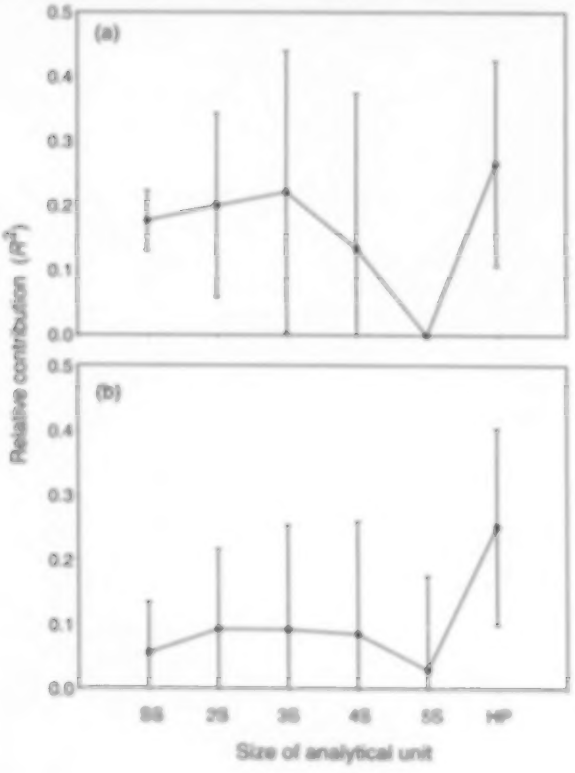
Fig. 6. Relative contributions of (*a*) the intrinsic variables and (*b*) the extrinsic variables to the three types of models.



tal variables contributing to the SC_3 model were the same as those used in the SC_1 models and accounted for 27% its among-patch variability. The density of submersed macrophytes, the size of habitat patches, and the fetch were the three variables correlated with SC_3.

Redundancy analysis performed on the fish community composition showed the presence of four main fish assemblages, each influenced by dominant environmental variables (Fig. 7). Only the first dimension was statistically significant, and accounted for 64.8% of the fish community variability. The first assemblage was represented by *S. atromaculatus* and *N. cryso*leucas and was correlated with the presence of woody debris. The two species were three (*S. atromaculatus*) and six times (*N. cryso*leucas) more abundant in patches with woody debris than in patches without this substrate (one-way multivariate analysis of variance (MANOVA), $F_{(2,41)} = 6.636$, $p < 0.003$). The second assemblage was characterized by *Perca flavescens*, *C. commersoni*, and *A. nebulosus*. These species were associated with the types of habitat and neighbouring patches (on the left side). They displayed higher densities in deep habitat patches and in highly vegetated patches with emergent macrophytes. Lower densities were found in habitat patches with high fetch values and with woody debris as substrates. The three species also displayed high densities when the neighbouring patches were highly vegetated with medium fetch values (~250 m). Highly exposed patches as neighbours had a negative impact on *Perca flavescens*, *C. commersoni*, and *A. nebulosus* densities. *Lepomis gibbosus* and *F. diaphanus* represented two single species assemblages and were associated with the fetch. *Fundulus diaphanus* was also correlated with the types of neighbouring patches. High densities of *F. diaphanus* were found when the neighbouring patches were composed of woody debris. When the neighbouring patches were characterized by high average depth and cabins on their riparian shore, *F. diaphanus* showed lower densities.

Table 5. Summary (mean R^2 and standard deviation (SD)) of the constant-multiple models developed for total fish density (TFD), relative biomass (RB), and size classes of fish (SC_x).

Group	Descriptor	*N*	Mean adjusted R^2 (SD)
1S	TFD	1	0.31 (0.00)
	RB	1	0.20 (0.00)
	SC_1	1	0.25 (0.00)
	SC_2	1	0.25 (0.00)
	SC_3	1	0.19 (0.00)
2S	TFD	2	0.38 (0.06)
	RB	2	0.27 (0.09)
	SC_1	2	0.40 (0.07)
	SC_2	2	0.29 (0.11)
	SC_3	2	0.24 (0.20)
3S	TFD	3	0.43 (0.25)
	RB	3	0.29 (0.15)
	SC_1	3	0.50 (0.06)
	SC_2	3	0.44 (0.01)
	SC_3	3	0.32 (0.05)
4S	TFD	4	0.42 (0.14)
	RB	4	0.31 (0.28)
	SC_1	4	0.56 (0.11)
	SC_2	4	0.43 (0.43)
	SC_3	4	0.37 (0.21)
5S	TFD	5	0.55 (0.17)
	RB	5	0.28 (0.30)
	SC_1	5	0.65 (0.19)
	SC_2	5	0.47 (0.05)
	SC_3	5	0.35 (0.27)
6S	TFD	6	0.60 (0.18)
	RB	6	0.52 (0.30)
	SC_1	6	0.78 (0.12)
	SC_2	6	0.57 (0.31)
	SC_3	6	0.44 (0.16)

The relative contribution of the intrinsic variables among the models ranged from 10% to 31% of the total variability of the fish community descriptors (Table 6). The extrinsic variables contributed from 13% to 38% of the total variability of the fish community descriptors. Among the extrinsic variables, the fetch (R^2 = 0.05–0.31) and the type of neighbour (R^2 = 0.13) were the two most important variables.

Randomly distributed patches

Models obtained using the habitat-patch approach defined by environmental characteristics displayed R^2 values that were 5- to 10-fold higher than models obtained by randomly dis-

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Table 6. Habitat-patch empirical models developed for total fish density (TFD), relative biomass (RB), and size classes of fish (SC_s).

Equation	Adjusted R^2	Intrinsic	Extrinsic
TFD = 0.079 + 0.029 S8 − 0.026 $\log_{10}$Fet − 0.017 U2	0.43***	0.25	0.18
RB = 0.838 − 0.931 $\log_{10}$Fet + 0.822 $\log_{10}$Sub	0.43***	0.25	0.18
SC_1 = 117.101 + 17.746 $\log_{10}$Fet − 10.576 $\log_{10}$Sub − 13.557 $\log_{10}$Size	0.49***	0.11	0.38
SC_2 = 14.942 − 6.931 S4 − 0.007 Trib − 0.103 Cov	0.44***	0.31	0.13
SC_3 = −8.511 + 6.635 $\log_{10}$Sub + 6.318 $\log_{10}$Size − 10.576 $\log_{10}$Fet	0.27***	0.10	0.17

Note: Variable codes are defined in Table 1. ***, $p \leq 0.001$.

Fig. 7. Ordination from the redundancy analysis (RDA) showing the relationships among fish species and environmental variables for the sampling-site approach. Only the first dimension was significant and accounted for 64.8% of the fish community variability. Legi, *Lepomis gibbosus*; Noct, *Notemigonus crysoleucas*; Seat, *Semotilus atromaculatus*; Fudi, *Fundulus diaphanus*; Amne, *Ameiurus nebulosus*; Peca, *Perca flavescens*; Caco, *Catostomus commersoni*; Cov, cover; Neigh-L, neighbour left; Hab, type of patch; S8, woody debris; S4 boulder (>250 mm); Fet, fetch.

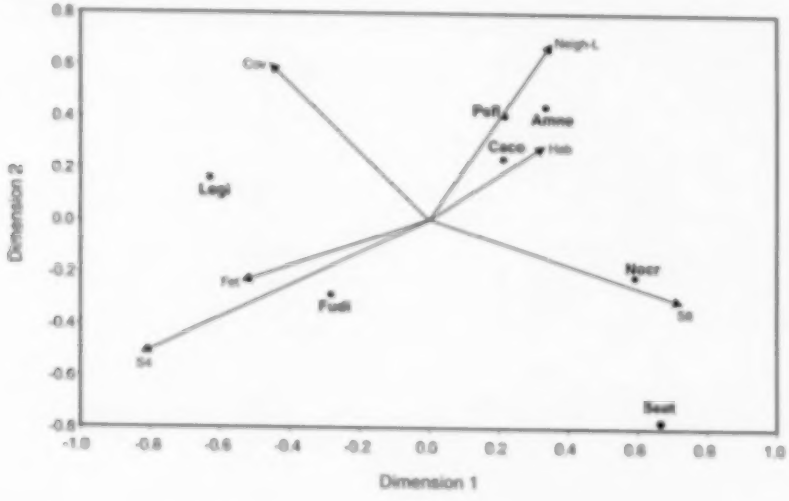

Table 7. Summary of the habitat-patch models obtained by using habitat patches randomly distributed in the littoral zone of the lake.

Random models	TFD	RB	SC_1	SC_2	SC_3	Species abundance
Mean R^2	0.066	0.043	0.067	0.069	0.069	0.139
SD	0.052	0.040	0.048	0.039	0.051	0.039
Percentile	1st	1st	1st	1st	1st	1st
Minimum	0.001	<0.001	<0.001	<0.001	<0.001	0.051
Maximum	0.346	0.245	0.286	0.345	0.263	0.325

Note: R^2 values for the habitat-patch models obtained with patches based on environmental characteristics are listed in Table 6.

tributed patches in the littoral zone of Lac Drouin (Table 7). The predictive power of the models developed with the environmentally defined patches always ranked in the first percentile of the permuted R^2 distributions. These results suggest that the environmental composition and the spatial arrangement of habitat patches are significantly influencing the fish community of Lac Drouin.

Discussion

Several studies have shown that littoral zones of lakes consist of a mosaic of habitat patches (Chick and McIvor 1994; Weaver et al. 1997; Grenouillet and Pont 2001). However, very few of them have tested the effect of the size of analytical units to study fish–habitat relationships, despite the evidence that patches may play an important role as

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functional units for different fish species and size classes (Weaver et al. 1997; Kocik and Ferreri 1998). Our study tested the effect of three approaches on the predictive power of fish habitat models. The use of the constant-multiple and the habitat-patch approaches instead of the sampling-site approach increased the predictive power of the habitat models from an average of 24% of the fish community variability (sampling-site approach) to 40% (average of constant-multiple approach) and 45% (habitat-patch approach). Our study also showed that the nature of the variables explaining the attributes of littoral fish communities changed with the size of the analytical units. The relative contribution of the extrinsic variables increased with the size of the analytical units. On average, the extrinsic variables represented 9%, 18%, and 21% of the total variability in the sampling-site, constant-multiple approach, and habitat-patch approach models, respectively.

Size of analytical units

The predictive power of fish–habitat models may be highly influenced by the merging of sampling sites, often because biological processes may occur at spatial scales broader than the sampling scale at which the study is performed (Cooper et al. 1998). For instance, the dispersal capability of a species may encompass several sampling units even within a specific period of a day (dawn, day, dusk). Consequently, the fish densities collected at the scale of the sampling site may be low and highly variable (Cooper et al. 1998). In such a case, the clustering of sampling sites may average out the intrinsic variability (Wiens 1989) and produce more robust predictive relationships between the fish and their environment (Poff 1997).

Because the predictive power of fish–habitat models is influenced by the sample size and the number predictive variables used in the model, we computed an adjusted R^2 that accounts for the variability of the two parameters. We also conducted bootstrap analyses on all the sizes of analytical units using the same sample size ($n = 12$). Results from these two analyses were highly correlated (Pearson $r = 0.68$, df = 13, $p = 0.005$) and confirmed that the observed increase in R^2 with the size of the analytical units was not a statistical artifact.

Predictions made by geostatistical studies of the effect of changing the size of the analytical units on the variance of aggregated units state that the variance of the aggregated samples should decrease linearly with the number of sampling units in an aggregated sample. As the size of the analytical units increases, the range of autocorrelation increases, while the variance and the proportion of noise in the data decrease (Bellehumeur and Legendre 1997). These predictions were partly supported by our results, for which increasing R^2 values were observed with the increase in size of the analytical units. However, if our results were solely explained by the geostatistical phenomenon, the constant-multiple approach would have systematically given the highest R^2 value for every model developed with the largest analytical units. This was not the case, and the coefficients of variation of the models developed using the constant-multiple approach were highly variable, ranging from 0% to 107%, with an average of 34.7%. We suggest that the high variability observed in the constant-multiple models may also be explained by the environmental characteristics on which the analytical units were based. For instance, a random merging of sampling sites may have no ecological relevance and, therefore, no consistent impact on the predictive power of the models. The merging of sites that occasionally resulted in the combination of similar contiguous habitats likely increased the R^2 of these models.

Why use habitat patches?

Littoral zones of lakes are known to display a diversity of microhabitats composed of a variety of physical and biological structures, such as rocky substrates and macrophyte beds (Werner et al. 1977; Chick and McIvor 1994). As opposed to a random process, such as the constant-multiple approach, the merging of the sites using the habitat-patch approach presumably matched the spatial structure of the heterogeneous environment of the littoral zone of Lac Drouin. We hypothesize that by using the clustering of contiguous sampling sites in patches of different sizes, the habitat-patch approach incorporated functional information on different habitat requirements of fish species.

The greater predictive power obtained with the models developed using habitat patches, compared with that obtained using the models developed using randomly distributed habitat patches, underlines the importance of the spatial arrangement of habitat patches in structuring littoral fish communities. This result also suggests that an arbitrary definition of conservation units may not be an optimal strategy to define areas that should be protected for conservation purposes. This is particularly interesting from a management perspective because conservation programs often focus on global targets, such as the percentage of total surface area to be protected (Chape et al. 2005). Our study emphasizes the importance of selecting a conservation area that contains a proper spatial configuration of environmental features (intrinsic and extrinsic).

Influence of the extrinsic variables

The sampling of environmental variables outside the sampling sites and the clustering of the sampling sites into habitat patches allowed us to create extrinsic variables that are rarely included in fish habitat models (Hanchin and Willis 2003). The relative contribution of these extrinsic variables was on average twice as high for the habitat models developed using the habitat-patch approach compared with models developed using the sampling-site approach. Although these spatial variables were particularly important in the habitat-patch approach, significant proportions of the explained variability using the sampling-sites approach were also related to the extrinsic variables (range = 4%–14% of the total variability explained). This suggests that commonly developed habitat models, using only intrinsic variables, would benefit from the inclusion of spatially structured variables measured outside the sampling site, such as fetch, distance to tributaries, and riparian use. To verify whether or not some extrinsic variables were acting as surrogates for some intrinsic variables, we conducted a correlation analysis between the two sets of variables. Results showed no strong correlations (maximum Pearson $r = 0.41$) between the two types of variables, indicating that the greater contribution of extrinsic variables observed as we increase the size of the analytical units is due to the nature of these variables and not to the effect of some surrogate variables.

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The greatest difference between the constant-multiple and the habitat-patch approaches was observed in the species composition (i.e., RDA analyses). Using the habitat-patch approach, the extrinsic variables accounted for nearly 60% of the total variance of the species composition, whereas these variables represented only 20% of the total variance of the species composition using the sampling-site approach. The type of habitat and the type of neighbour were the two most important variables differentiating the two approaches. Our results showed that habitat patches displaying similar intrinsic environmental characteristics might differ in their species composition and fish density, depending on the type of environmental characteristics of the surrounding patches (or neighbours; Bohnsack 1991). Our study corroborates the results of Weaver et al. (1997), who found that the integration of variables describing the spatial arrangement of habitat within the littoral zone of the lake likely enhanced the understanding of fish–habitat relationships.

Size-structured patchiness

The size of the habitat patch was an important predictor of the fish–habitat models and principally in the models developed for the size structure of the fish community. The density of small fish was lowest in large patches, whereas the opposite trend was observed for large fish. It may be argued that fish density, irrespective of the size class, would increase with the size of the patches. Habitats distributed in larger patches may display a wider range of environmental conditions compared with smaller patches, thus decreasing interspecific competition and thereby supporting greater densities of fish (Dunham et al. 2001). However, our results did not support this expectation. We may argue that the size of a habitat patch is organism dependent (Wu and Loucks 1995). For instance, a habitat patch of 150 m^2 could be perceived either as small or large, depending on the size of the fish that occupies it. In our study, the minimum size of the fish in SC_1 (30 mm) was 10 times smaller than the maximum size of fish from SC_3 (320 mm). Furthermore, differences in the use of the size of a habitat between the small and large size classes might be the result of scale-dependent responses (Wiens 2002). Small fish species may respond to fine scale habitat variation, whereas large species responded to habitat variation at a broader spatial scale. The spatial succession of small, structurally complex patches, such as those observed in our study, may be more appealing to small fish rather than larger patches would be, because small patches provide both shelter and higher densities of cladocerans on the edges of habitat patches (small patches = higher edge/surface ratio; Nurminen and Horppila 2002).

Together with the size of habitat patches, fetch and density of submersed macrophytes influenced the smallest and the largest size classes of the fish community in different ways. Small fish were associated with exposed patches with low density of submersed macrophytes, whereas large fish were associated with protected patches with a high density of submersed macrophytes. Keddy (1983) demonstrated that intermediate fetch values may be beneficial to macrophyte growth and that species composition of macrophyte beds may vary among exposed and protected shores. Although we did not distinguish macrophyte species, it is possible that both the exposed and protected shores differed in their macrophyte composition and offered a different quality of habitat to the two size classes of fish (Grenouillet and Pont 2001). The linear relationship between the size of the fish and the fetch seemed to contradict the findings of Randall et al. (1996), who observed a nonlinear relationship between fetch and size of the fish. However, their study was conducted in small bays of Lake Ontario, where fetch reached values three times larger than in Lake Drouin. When similar fetch values were compared, both studies observed a negative relationship between the size of the fish and the fetch. Larger fish were most abundant with low fetch values, whereas smaller fish were most abundant with high fetch values. These results suggest that fetch indirectly affected the fish community of Lac Drouin, either by its involvement in the determination of benthic production (Burkholder 1992; Cyr 1998) or by its participation in the structuring of littoral habitats (e.g., macrophyte beds; Keddy 1983). Fetch may also indirectly affect fish distribution in lakes by influencing the thermal structure (warmer temperature downwind; Finlay et al. 2001). However, according to Finlay et al. (2001), the influence of wind on the thermal regime of small lakes (<1 km^2), such as Lac Drouin, is still unknown. Given the small variability in temperature among the sampling sites (1.31 °C) and given that the temperature was not significantly correlated with fetch ($r = 0.20$, $p = 0.06$), we suggest that in Lac Drouin, fetch did not have an indirect influence on the fish community via the temperature. Much remains to be done to fully elucidate the mechanisms underlying the interactions that may exist among fish distribution patterns and environmental features. However, our work does indicate that a landscape context provided by the use of habitat patches as analytical units, the attention to intrinsic and extrinsic environmental features, and the effect of the size and the spatial arrangement of habitat patches should be considered in studies that focus on the modelling and conservation of fish habitats in the littoral zone of lakes.

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Appendix A

Table A1. Empirical models developed using the constant-multiple approach for total fish density (TFD), relative biomass (RB), and size classes of fish (SC_s).

	Equation	Adjusted R^2	Local	Spatial
1S	TFD = 2.767 − 0.001 *Size* − 0.133 $\log_{10}$Fet − 0.376 O_2 + 0.006 Sub	0.31***	0.10	0.21
	RB = 53.261 − 0.014 *Size* − 1.955 $\log_{10}$Fet − 7.628 O_2	0.20***	0.07	0.13
	SC_1 = −112.545 + 12.101 Fet − 5.246 Depth + 32.787 O_2	0.25***	0.13	0.12
	SC_2 = 10.458 − 6.457 S4 − 5.779 $\log_{10}$Fet + 3.854 S8 − 11.927 Pier	0.25***	0.19	0.06
	SC_3 = 0.387 + 5.135 Depth − 4.482 $\log_{10}$Fet	0.19***	0.15	0.04
2S	TFD = 0.249 − 2.947×10^{-4} *Size* + 0.038 S8 − 0.036 S4	0.33***	0.18	0.15
	RB = −1.579 + 1.928 Depth + 1.492 $\log_{10}$Emer	0.21***	0.21	0.00
	SC_1 = 89.730 − 8.500 Depth + 7.826 S4 + 0.008 Trib + 6.084 U4	0.45***	0.33	0.12
	SC_2 = 13.384 − 6.403 S4 − 0.005 Trib	0.22***	0.15	0.07
	SC_3 = −6.076 + 7.921 Depth	0.25***	0.25	0.00
2S	TFD = 0.244 − 3.239×10^{-4} *Size* − 0.047 S4 + 0.030 S8 + 0.031 U1	0.42***	0.21	0.21
	RB = 6.745 − 1.740 S4 − 0.011 *Size* + 1.455 U1	0.33***	0.14	0.19
	SC_1 = 77.935 + 9.457 S4 + 9.847 $\log_{10}$Fet	0.35***	0.24	0.11
	SC_2 = 8.661 − 5.226 S4 + 5.831 $\log_{10}$Emer − 0.005 Trib	0.37***	0.28	0.09
	SC_3 = 0.225 + 5.332 Depth − 4.831 $\log_{10}$Fet	0.22***	0.16	0.04
3S	TFD = 0.327 − 3.291×10^{-4} *Size* − 0.047 S4 + 0.051 U3 + 0.122 Litt	0.61***	0.18	0.43
	RB = 8.115 − 0.008 *Size* − 2.275 $\log_{10}$Fet + 0.183 Sub	0.42***	0.10	0.31
	SC_1 = 74.877 + 8.737 $\log_{10}$Fet + 8.517 S4 + 6.370 U4	0.50***	0.14	0.36
	SC_2 = 28.660 − 5.842 S4 − 0.025 *Size* − 5.585 $\log_{10}$Fet	0.43***	0.22	0.21
	SC_3 = −5.848 + 9.386 Depth − 3.982 S8	0.33***	0.33	0.00
3S	TFD = 0.110 + 0.050 S8 − 0.040 S4 − 1.751×10^{-4} *Size*	0.53***	0.43	0.10
	RB = 2.248 − 1.517 S4 + 1.282 S8	0.33***	0.33	0.00
	SC_1 = 74.558 + 10.197 $\log_{10}$Fet + 7.770 U4 + 7.869 S4	0.56***	0.12	0.44
	SC_2 = 211.699 − 5.262 S4 − 0.006 Trib − 32.392 O_2	0.44***	0.35	0.09
	SC_3 = −6.802 + 8.359 Depth	0.27***	0.27	0.00
3S	TFD = 0.151 − 0.045 S4	0.14***	0.14	0.00
	RB = 3.280 − 1.410 S4	0.12***	0.12	0.00
	SC_1 = 83.965 + 12.076 $\log_{10}$Fet + 10.020 U4 − 12.679 $\log_{10}$Emer	0.44***	0.14	0.30
	SC_2 = 3.874 + 11.836 $\log_{10}$Emer − 6.132 $\log_{10}$Fet − 3.852 U4	0.44***	0.23	0.21
	SC_3 = 12.715 − 5.995 U4 − 5.934 $\log_{10}$Fet	0.37***	0.00	0.37
4S	TFD = 2.446 − 0.379 O_2 + 0.050 U3	0.33***	0.19	0.14
	RB = ns			
	SC_1 = 88.556 + 13.063 $\log_{10}$Fet + 7.768 S4 + 11.337 S9 − 7.585 Depth	0.69***	0.37	0.32
	SC_2 = 9.232 − 5.687 S4 + 5.645 U3	0.46***	0.30	0.16
	SC_3 = −8.976 + 9.740 Depth	0.37***	0.37	0.00
4S	TFD = 0.257 − 0.060 S4 − 1.652×10^{-4} *size* + 0.053 U1	0.53***	0.27	0.26
	RB = 1.685 − 2.165 S4 + 2.308 U1	0.38***	0.19	0.19
	SC_1 = 71.844 + 9.634 S4 + 10.731 U2	0.60***	0.39	0.21

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Table A1 (*continued*).

	Equation	Adjusted R^2	Local	Spatial
	SC_2 = 9.449 – 5.813 S4 + 7.112 U3	0.45***	0.22	0.23
	SC_3 = 15.858 – 8.513 U2 – 4.390 S4	0.67***	0.17	0.50
4S	TFD = 0.097 + 0.053 S8	0.28***	0.28	0.00
	RB = 3.398 – 1.784 U4 + 1.803 $\log_{10}$Emer – 0.001 Trib – 0.977 S4	0.66***	0.26	0.40
	SC_1 = 71.293 + 10.556 U4 + 7.607 S4 + 0.009 Trib	0.51***	0.11	0.40
	SC_2 = 4.463 – 7.178 U4 + 9.580 $\log_{10}$Emer	0.37***	0.18	0.19
	SC_3 = 9.615 – 5.435 U4	0.20***	0.00	0.20
4S	TFD = 0.103 + 0.045 S8 + 0.045 U3 – 0.036 S4	0.55***	0.35	0.20
	RB = 3.244 – 1.489 S4	0.19***	0.19	0.00
	SC_1 = 77.447 + 10.351 $\log_{10}$Fet + 8.032 S4	0.44***	0.14	0.30
	SC_2 = 9.377 – 6.053 S4 + 6.367 U3	0.46***	0.29	0.17
	SC_3 = –7.511 + 8.774 Depth	0.25***	0.25	0.004
5S	TFD = 0.177 – 0.048 S4 – 0.042 U4	0.43***	0.22	0.21
	RB = 4.448 – 1.867 U4 – 1.537 S4	0.59***	0.27	0.32
	SC_1 = 77.336 + 11.054 $\log_{10}$Fet – 11.960 $\log_{10}$Emer + 7.894 U4 + 6.344 U2 + 5.238 S4	0.85***	0.24	0.61
	SC_2 = 9.519 – 6.246 S4 + 5.889 U3	0.47***	0.19	0.06
	SC_3 = 7.896 + 4.090 Depth – 4.894 $\log_{10}$Fet – 3.788 U4 – 3.891 U2	0.76***	0.46	0.30
5S	TFD = 2.389 – 0.365 O_2 – 4.017×10^{-5} Trib	0.22***	0.22	0.00
	RB = 9.152 – 0.006 Size	0.19***	0.00	0.19
	SC_1 = 46.118 + 10.606 U2 + 9.642 $\log_{10}$Fet + 5.508 S4 – 0.02 Size	0.80***	0.09	0.71
	SC_2 = 8.782 + 8.026 U3 – 3.871 S4	0.50***	0.12	0.38
	SC_3 = 14.633 – 8.544 U2	0.31***	0.00	0.31
5S	TFD = 0.268 – 1.658×10^{-4} Size – 0.035 S4 + 0.177 Litt + 0.046 U3	0.72***	0.31	0.42
	RB = ns			
	SC_1 = 74.712 + 12.925 $\log_{10}$Fet + 6.514 S4 + 10.216 S9	0.70***	0.35	0.35
	SC_2 = 8.907 + 7.489 U3 – 4.345 S4	0.52***	0.17	0.35
	SC_3 = ns			
5S	TFD = 0.101 – 0.042 S4 + 0.060 U3 + 0.047 S8	0.73***	0.44	0.29
	RB = ns			
	SC_1 = 76.307 + 10.610 $\log_{10}$Fet + 7.449 S4	0.44***	0.18	0.26
	SC_2 = 8.971 + 7.027 U3 – 4.268 S4	0.45***	0.15	0.30
	SC_3 = –9.793 + 10.166 Depth	0.28***	0.28	0.00
5S	TFD = 0.158 – 0.059 S4	0.48***	0.48	0.00
	RB = 1.724 – 2.878 U4 + 3.553 $\log_{10}$Emer	0.61***	0.35	0.26
	SC_1 = 99.937 + 10.331 S4 – 12.058 Depth	0.48***	0.48	0.00
	SC_2 = 11.624 – 7.257 S4	0.38***	0.38	0.00
	SC_3 = –11.218 + 11.026 Depth	0.38***	0.38	0.00
6S	TFD = 2.844 – 0.046 S4 – 0.435 O_2 – 5.442×10^{-5} Trib	0.84***	0.70	0.14
	RB = 4.663 – 1.608 S4 – 1.623 U4	0.48***	0.24	024
	SC_1 = 65.243 + 10.961 S4 + 12.312 U2 + 0.007 Trib	0.85***	0.34	0.51
	SC_2 = 23.612 – 6.482 S4 + 3.631 U3 – 5.155 $\log_{10}$Fet – 0.008 Size	0.88***	0.49	0.39
	SC_3 = 15.010 – 9.198 U2	0.33***	0.00	0.33
6S	TFD = 1.871 – 0.034 S4 + 0.040 U3 – 0.283 O_2	0.73***	0.50	0.23
	RB = ns			
	SC_1 = 67.067 + 11.724 U2 + 8.816 S4 + 7.521 $\log_{10}$Fet	0.81***	0.37	0.44
	SC_2 = 13.117 + 6.458 U3 – 4.405 S4 – 4.563 U2	0.75***	0.19	0.56
	SC_3 = –5.836 + 7.775 Depth	0.22***	0.22	0.00
6S	TFD = 2.960 – 0.464 O_2 + 0.046 U3	0.57***	0.35	0.22
	RB = 0.965 – 2.835 U4 + 3.616 $\log_{10}$Emer + 0.947 S8	0.90***	0.49	0.41
	SC_1 = 88.149 + 19.116 U3 – 18.773 $\log_{10}$Emer – 4.116 S1	0.88***	0.44	0.44
	SC_2 = 6.783 – 6.060 U3	0.26***	0.00	0.26
	SC_3 = 13.463 – 8.760 U4	0.65***	0.00	0.65
6S	TFD = 0.150 + 0.047 U3 – 0.042 U4	0.46***	0.00	0.46
	RB = 2.139 – 2.394 U4 + 2.816 $\log_{10}$Emer	0.68***	0.36	0.33
	SC_1 = –26.732 + 29.410 $\log_{10}$Fet + 0.084 Size – 0.019 Trib	0.70***	0.00	0.70

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Table A1 (*concluded*).

	Equation	Adjusted R^2	Local	Spatial
	$SC_2 = 6.794 + 6.019\ U3$	0.27***	0.00	0.27
	$SC_3 = 12.036 - 6.814\ U4$	0.47***	0.00	0.47
6S	$TFD = 0.153 - 0.045\ S4$	0.37***	0.37	0.00
	$RB = 4.052 - 1.382\ S4 - 1.083\ U4$	0.49***	0.33	0.16
	$SC_1 = 44.005 + 14.641 \log_{10}Fet - 0.026\ Size$	0.57***	0.00	0.57
	$SC_2 = 6.612 + 6.754\ U3$	0.34***	0.00	0.34
	$SC_3 = 13.307 - 6.327 \log_{10}Fet - 4.243\ U2$	0.56***	0.00	0.56
6S	$TFD = 0.166 - 0.064\ S4$	0.64***	0.64	0.00
	$RB = 5.147 - 1.948\ S4 - 1.631\ U2$	0.57***	0.44	0.13
	$SC_1 = 67.237 + 10.264\ S4 + 10.456\ U2 + 5.490 \log_{10}Fet$	0.86***	0.49	0.37
	$SC_2 = 7.955 - 6.745\ S4 + 7.099\ U3 + 3.394\ S3$	0.89***	0.19	0.06
	$SC_3 = 15.055 - 9.114\ U2$	0.41***	0.00	0.41

Note: Variable codes are defined in Table 1. ns, not significant. ***, $p \leq 0.001$.

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Size-structured patterns of piscivory of the longfin inshore squid (*Loligo pealeii*) in the mid-Atlantic continental shelf ecosystem

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Abstract: The longfin inshore squid (*Loligo pealeii*) dominates the landings in the USA mid-Atlantic continental shelf region, yet the potential ecological effects of harvesting this species are not known. Because squid feed on a wide variety of prey items, including juvenile stages of commercially important fish species, a full exploration on the predatory role of squid in this ecosystem is warranted. We examined the seasonal diet contents of *L. pealeii* and evaluated the importance of size constraints in governing patterns of piscivory. Our analyses showed that piscivory was dictated by size constraints, with larger squid demonstrating higher rates of piscivory than small squid. Squid were piscivorous at smaller sizes in the winter and spring than during the summer and autumn. Also, the frequency of piscivory was highest during the winter and spring, coincident with the time period when the number of vulnerable prey species was greatest. Our findings suggest that the frequency and intensity of piscivory are likely to be related to the duration of time that prey are vulnerable to predation, which in turn is dictated by the relative body sizes of *L. pealeii* and juvenile fishes.

Résumé : Le calmar totam (*Loligo pealeii*) prédomine dans les débarquements dans la région de la plate-forme continentale de l'Atlantique moyen aux É.-U.; cependant, les effets écologiques potentiels de la récolte de cette espèce sont inconnus. Il est nécessaire d'explorer à fond le rôle de prédateur des calmars dans cet écosystème, parce que ceux-ci utilisent une gamme étendue de proies, y compris les jeunes stades de poissons d'importance commerciale. Nous avons analysé la composition du régime alimentaire de *L. pealeii* en fonction des saisons et évalué l'importance des contraintes reliées à la taille dans l'établissement des patrons d'ichtyophagie. Nos analyses montrent que l'ichtyophagie est contrôlée par des contraintes reliées à la taille et que les calmars de plus grande taille ont des taux d'ichtyophagie plus importants que les petits calmars. Les calmars deviennent ichtyophages à des tailles plus faibles en hiver et au printemps qu'en été et en automne. De plus, la fréquence de l'ichtyophagie est plus élevée en hiver et au printemps, ce qui coïncide avec la période pendant laquelle le nombre d'espèces de proies vulnérables est le plus grand. Dans leur ensemble, nos résultats indiquent que la fréquence et l'intensité de l'ichtyophagie sont susceptibles d'être reliées à la durée de la période de vulnérabilité des proies à la prédation, elle-même déterminée par les tailles corporelles relatives de *L. pealeii* et des jeunes poissons.

[Traduit par la Rédaction]

Introduction

It is widely acknowledged that squid are a key component in marine food webs, as evidenced by their importance as prey items (Clarke 1996; Klages 1996; Piatkowski et al. 2001) and as predators (Sauer and Lipinski 1991; Rodhouse and Nigmatullin 1996; Santos and Haimovici 1998). Squid play a central role in the transfer of energy from lower to higher trophic levels (Vovk 1974; Nixon 1987; O'Dor and Wells 1987), and their trophic relationships can be quite complex, as squid are consumed by fishes when they are young and then consume those same predators as they grow older (Vovk 1974; Hanlon and Messenger 1996). Squid predation has been suggested as a significant source of prerecruit mortality in fish (Maurer and Bowman 1985) and may serve as a potential constraint on the recruitment success of commercially targeted fish, especially during years of high squid abundance (Dawe 1988; Rodhouse and Nigmatullin 1996).

Time series of fishery landings data show that in recent years cephalopod landings, of which squid are the majority, have dramatically increased, while groundfish landings have remained stable or declined (Caddy and Rodhouse 1998). The commercial fishery in the USA mid-Atlantic continental shelf region is an example of this trend. Landing approximately 100 000 t·year^{-1} (National Oceanographic and Atmospheric Administration (NOAA) Fisheries 2002), this fishery is composed of a diverse assemblage of groundfish, small pelagics, and squids. The domestic fishery for longfin inshore squid, *Loligo pealeii*, developed within the last

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25 years and constitutes a dominant percentage (15%, NOAA Fisheries 2002) of the total commercial landings of nektonic species in the mid-Atlantic region. Notably, in New York, the landings of *L. pealeii* nearly doubled over the 1990s from 2890 to 5641 t and have dominated the total landings since 1999 (20%, NOAA Fisheries 2002), an indication of the increasing importance of their role in this fishery.

The ecological effects of squid harvesting are not known. Past studies provide some suggestion that *L. pealeii* play a pivotal role in the mid-Atlantic food web. Predators of *L. pealeii* include *Pomatomus saltatrix*, *Scomber scombrus*, *Melanogrammus aeglefinus*, *Pollachius virens*, *Merluccius bilinearis*, *Urophycis* sp., and *Paralichthys dentatus* (Langton and Bowman 1977; Lange 1980; Bowman et al. 2000). Thus, fisheries targeting *L. pealeii* might have an unintended negative impact on the productivity of other commercially valuable stocks. However, diet analyses have also found that *L. pealeii* prey upon juvenile gadids, merluccids, clupeids, and scombrids (Vovk 1972, 1985; Macy 1982), suggesting the possibility of positive effects of squid fishing on finfish production. Thus, not only the magnitude but also the direction of the effect of squid fisheries on other fisheries in this region is difficult to predict without detailed information on the interactions between squid and fishes in the food web.

Any attempt to explore food web interactions involving squid needs to explicitly account for the size structure of these interactions. Size-structured interactions can have substantial effects on predator–prey dynamics (Persson et al. 1996), and many predators exhibit ontogenetic, size-dependent patterns in predation (Polis et al. 1996; Scharf et al. 2000; Juanes et al. 2002). Squid are no exception to this rule, as several studies on squid feeding habits have convincingly documented the influence of body size on diet composition (Maurer and Bowman 1985; Collins et al. 1994; Lordan et al. 1998). These shifts are possibly related to size constraints on capturing and handling prey, as indicated by the relation between the ranges of prey sizes consumed with squid body size (Rocha et al. 1994; Collins and Pierce 1996; Phillips et al. 2003). Given that squid are likely to prey upon rapidly growing larval or juvenile stages of fish, we should expect that the frequency and intensity of piscivory would be limited by the duration of time that these fish are within a size range in which they are vulnerable to squid. Moreover, we should also expect that the magnitude of predation would be dictated by the size structure of the squid population. If these hypotheses are true, then fishing might have profound effects on squid–fish interactions by inducing shifts in the size structure of squid populations. Thus, there may be more substantial effects of fishing on trophic interactions mediated by size-selective fishing and predation that might not be apparent through modeling exercises that treat predators and prey as homogeneous pools (Jennings et al. 2002).

In this study, we examined the seasonal stomach contents of *L. pealeii* and estimated the sizes of fish and squid prey to provide answers to the following questions: How is predation on fish by squid governed by size constraints? How does the ontogeny of piscivory change seasonally? Can size-constrained predation explain the patterns of piscivory? Insights derived from this study can be used in future research to construct size-structured food web models, quantify the predatory impact of squid on fish populations, and evaluate the effects of squid predation under alternative management strategies.

Materials and methods

Collection of *L. pealeii* stomach samples

Approximately 3000 squid were collected from the mid-Atlantic continental shelf waters from April 2002 to May 2003 (Fig. 1). Squid were collected from waters offshore (>8 km) of New York and New Jersey on a monthly basis, with the exception of July, October, and November. Squid samples were obtained from bottom trawl surveys conducted by the NOAA National Marine Fisheries Service (September 2002, February and March 2003), New Jersey Department of Environmental Protection (June 2002), and from regional commercial fishing vessels (April, August, December 2002 and January–April 2003). Squid collected from bottom trawl surveys (0.5 inch mesh cod-liner; 1 in = 25.4 mm) were sampled across a wide area of the study region and were collected farthest from shore during the winter (depth: 59–217 m) and early spring (depth: 81–247 m) and closer to shore during summer (depth: 14–26 m) and autumn (depth: 11–125 m). Squid sampled from fishing vessels (min. 1.875 inch diamond mesh) during the winter and early spring were captured within the Hudson Canyon region (depth: 146–274 m), while the late spring and summer samples were captured in shallower waters south of Long Island (depth: ~30 m). These sample locations follow the natural inshore and offshore migration patterns of *L. pealeii*.

Squid were sampled from commercial vessels with the intention of collecting a wide size range of squid throughout each season to account for seasonal and ontogenetic shifts in diet compositions. In research cruises, squid were haphazardly subsampled from tows. For all squid sampled, body mass was weighed to the nearest 0.01 g, dorsal mantle length was measured to the nearest millimetre, and stomach contents were frozen until ready for identification by microscopy. Hard parts of prey, such as otoliths, scales, bones, statoliths, and beaks that remained in the stomachs, were used to identify prey of the collected squid (Vinogradov and Noskov 1979; Santos and Haimovici 1998). Crustaceans were also identified by eyes, appendages, mandibles, and exoskeletons (Karpov and Cailliet 1978; Santos and Haimovici 1998). Prey items were initially grouped by visual identification of hard parts and soft tissues as fish, squid, crustaceans, or unknown and categorized as fresh, partially digested, or well digested. Once identified, wet weights and lengths (when applicable) of each prey item were recorded, and the hard parts were stored in 90% ethanol for subsequent taxonomic classification.

General diet analyses

We quantified the diet composition of *L. pealeii* by calculating the percent frequency of occurrence of each prey item in the squid stomach contents. Other measures (e.g., percent by number or mass) are essentially impossible because squid masticate their food. To identify the order (or lowest taxon) of prey consumed by *L. pealeii*, the morphological features and size ratios of the digested otoliths were compared with those presented in guidebooks (Brodeur 1979; Härkönen

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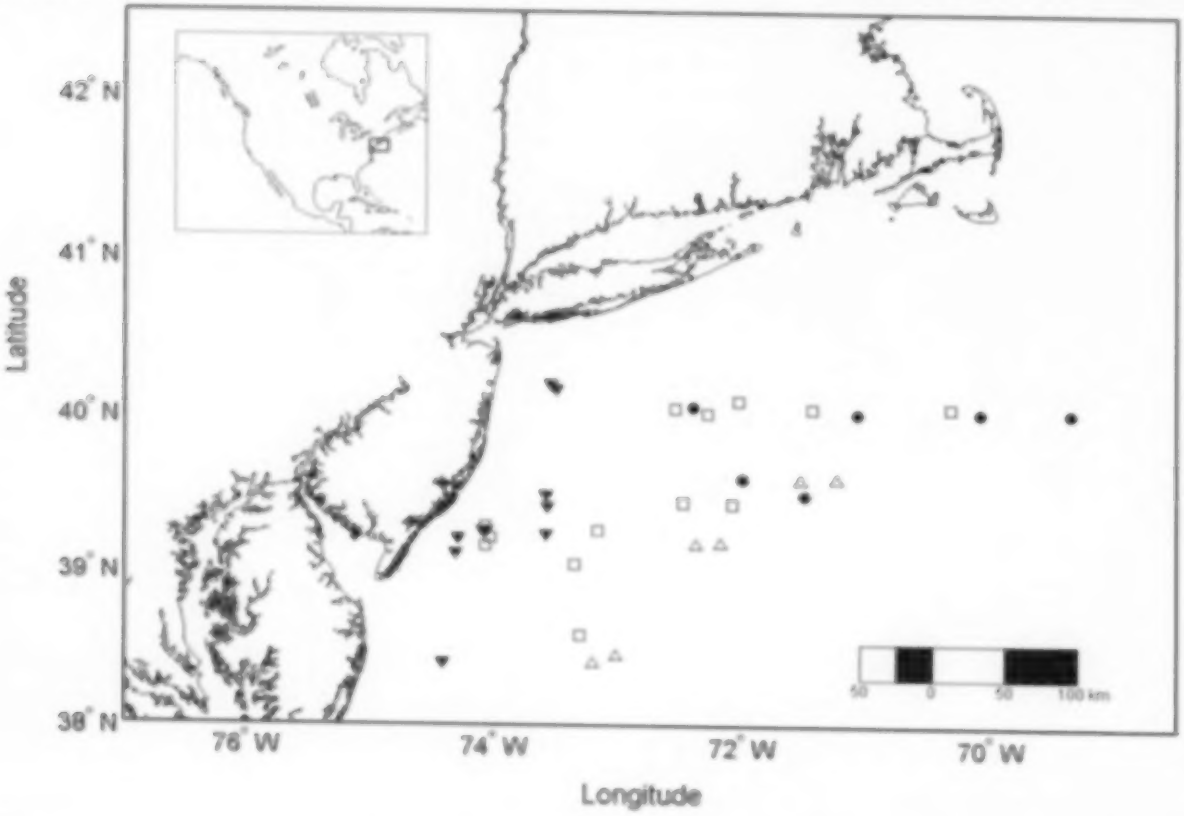
Fig. 1. Location of sampling sites for *Loligo pealeii* collected from National Marine Fisheries Service (NMFS) and New Jersey Department of Environmental Protection (NJDEP) bottom trawls surveys during the winter (solid circles), spring (open triangles), summer (solid, upsidedown triangles), and autumn (open squares). Inset of North America show the sampling area off the coast of New York and New Jersey, USA.



1986) as well as with lab reference collections. No attempt was made to match otolith pairs and each otolith was treated as a single prey item. Otoliths were classified to order or family only if the otoliths were indistinguishable from the references. Otoliths that were well digested and lacked distinctive features required for classification were categorized as unknown. To further support our classifications, we compared our findings with the expert opinions and extensive reference collection at the Fishery Biology Investigation Laboratory (Woods Hole, Massachusetts). Squid species consumed by *L. pealeii* were also identified by comparing the features of the lower squid beaks found in the stomach contents with guidebooks (Clarke 1986) and lab reference collections. *Loligo* sp. and *Illex* sp. are the only species of squid that inhabit the study region, and their lower beak features are quite distinct.

Determination of prey sizes

To determine the prey sizes of the ingested fish, the lengths of the digested otoliths were measured to the nearest 0.1 mm. Prey sizes were calculated using otolith length to body length relationships for each genus (Table 1). When otoliths could not be classified to genus, we determined prey sizes by averaging the estimated body sizes of all species within that order or family for which regressions were available. This was only possible when regression equations of the different species were similar. The sizes of ingested squid were also determined using the lower beak rostral length and dorsal mantle length relationship for *L. pealeii* (Gannon et al. 1997) (Table 1). When only upper beaks remained in the stomach contents, the upper beak rostral lengths were used to estimate prey sizes as done by previous authors (Dawe et al. 1998). The rostral lengths of squid upper and lower beaks were measured to the nearest 0.1 mm.

We analyzed the relationship between squid and prey sizes using quantile regression (version 8.2, StataCorp Statistical Software, College Station, Texas). This technique allowed us to estimate the relationship between predator length and minimum or maximum prey sizes by analyzing the edges of scatter diagrams (Scharf et al. 1998, 2000). This regression procedure differs from the least squares technique, as the regression quantiles are determined by minimizing the sums of the absolute values of residuals rather than by minimizing the sums of squares. The 90th and 10th quantiles were used as upper and lower bound regression quantiles in this analysis and were chosen based on sample size (Rogers 1992;

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Table 1. Parameters of the otolith size – fish size (mm) regression used to estimate sizes of fish ingested by *Loligo pealeii*.

Prey	*a*	*b*	Transform	Reference
Loligo pealeii	1.767	1.4	logL	Gannon et al. 1997
Benthosema sp.	–3.3272	25.0114	TL	Markaida and Sosa-Nishizaki 2003
Ammodytes americanus	–4.377	9.024	FL	Bowen and Harrison 1994
Sebastes sp.	3.1273	1.436	lnFL	Hunt 1992
Maurolicus muelleri	9.82	28.75	FL	Härkönen 1986
Melanogrammus aeglefinus	0.94834	1.38	logFL	Härkönen 1986
Merlangius merlangus	–11.936	19.7	FL	Härkönen 1986
Urophycis tenuis	0.18327	1.1456	logFL	Clay and Clay 1991
Pollachius virens	1.8117	1.6251	lnFL	Hunt 1992
Merluccius bilinearis	2.9475	1.0276	lnFL	Hunt 1992

Note: The general form of the model was $L' = a + bOL'$, where L' and OL' are the actual lengths or log-transformed lengths, respectively. A lower beak rostral length – dorsal mantle length (mm) regression equation was used to estimate the sizes of squid consumed by *L. pealeii*.

Scharf et al. 1998). Additionally, we used the Student's *t* test to compare the slopes of the upper bound regression quantiles to determine whether maximum prey size differed between fish and cannibal prey (Scharf et al. 2000; Juanes 2003).

Ontogenetic shifts in diet compositions

To detect ontogenetic shifts in the diet composition of *L. pealeii*, we employed logistic regression analyses. We categorized *L. pealeii* diet into fish and squid and assigned a zero or one to each category depending on whether each respective prey item was absent or present in each stomach sample. Logistic regression was used to relate the probability of occurrence of a specific prey item (fish or squid) to squid mantle length (L) (20–280 mm), but we introduced more biologically meaningful parameters to replace the standard logistic regression parameters. Specifically, we define F_{max} as the maximum probability of piscivory, L_{50} is length at which the predicted rate of piscivory is 50% of the maximum (generally reflects size at onset of piscivory), and δL as the difference between L_{50} and L_5 (the length at which the predicted rate of piscivory is 5%). The δL value gives an indication as to the abruptness of the onset of piscivory. Small values indicate very abrupt ontogenetic shifts and large values indicate gradual shifts. Given these parameters, the probability of piscivory (P) equals

$$(1) \qquad P = \frac{F_{max}\exp[Z(-L_{50} + L)]}{1 + \exp[Z(-L_{50} + L)]}$$

$$Z = \frac{2.94}{\delta L}$$

Maximum likelihood estimates of F_{max}, L_{50}, and δL were estimated numerically using Solver in Microsoft Excel® (Microsoft Corporation, Redmond, Washington).

Loligo pealeii reside in offshore water during the winter–spring and nearshore during the summer–autumn. We compared ontogenetic shifts in piscivory between these periods by calculating the 90% prediction intervals for the probability of piscivory through parameterization of eq. 1 using data collected during these two periods. Prediction intervals were calculated using a grid-based description of the likelihood surface with respect to F_{max} and L_{50}, using the best-fitting value of δL for each point along the grid. Based on these likelihoods, we calculated the expected probability of piscivory for each element of the grid and generated the 5th, 50th, and 95th percentiles of P based on the cumulative likelihood function. This is equivalent to a Bayesian credibility interval under the special condition of a uniform (non-informative) prior on F_{max}, L_{50}, and δL.

Further, to evaluate whether seasonal patterns of piscivory were linked to prey size constraints, we estimated the number of species of juvenile fish that were within the prey size spectra of the squid population during each season. This analysis proceeded in four steps. First, squid length-frequency distributions were calculated from the squid sampled by bottom trawl surveys during this study. Second, we calculated the prey size spectrum for each squid length using the upper and lower bound quantile regression equations determined in this study. Third, we estimated the sizes of each potential age-0 fish prey in each season based on published literature (Sherman et al. 1984; Quinonez-Velazquez 1999; Clay et al. 1989; Able et al. 1990; Comyns and Grant 1993; Morse and Able 1995; Able and Fahay 1998; Cargnelli et al. 1999*a*, 1999*b*; Chang et al. 1999*a*, 1999*b*; Packer et al. 1999; Steimle et al. 1999; Steves et al. 1999; Steves and Cowen 2000; Lock and Packer 2004). We constrained this question to juvenile fish that are known to spatially and temporally overlap with *L. pealeii*. Lastly, based on the predator and prey sizes, we estimated the number of species of juvenile fish vulnerable to predation by squid of each length category.

Results

Description of *L. pealeii* samples

Approximately 3000 squid were sampled from both commercial and research vessels throughout the spring (n = 911), summer (n = 868), and winter (n = 503). In the autumn (n = 744), squid were collected only by research vessels because the regional squid fishery was closed owing to an enforced quota limit. Squid sizes ranged from 20 to 360 mm, with an average size of 115 ± 58 mm. The squid samples collected by bottom trawl surveys were dominated by smaller sized

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squid in June and September and by larger size squid during the month of February. In March, the size distribution of *L. pealeii* was more homogeneous. The seasonal length distributions of squid collected in this study were similar to those described in some past studies that analyzed the population structure of *L. pealeii* (Macy 1982; Brodziak and Macy 1996; Hatfield and Cadrin 2002).

General diet analyses

Identifiable prey items were found in 45.7% of the squid stomachs, while the unidentifiable prey constituted 28.2% of the stomach samples. The remaining squid stomachs (26.1%) were empty. The high percentage of unknown prey is a result of the large number of unknown diet items found in the stomachs of small squid (<80 mm). Approximately 60% of the total unknown prey items were found in the stomachs of small squid. The diet contents of the smaller squid were often well digested and difficult to identify, possibly an effect of their high digestion rates and (or) feeding behavior. Of the total portion of identifiable prey, squid comprised the highest percentage of diet items followed by crustaceans and fish (Table 2). We also found a higher percentage of single prey items in comparison with multiple prey items in *L. pealeii* stomach contents (Table 2).

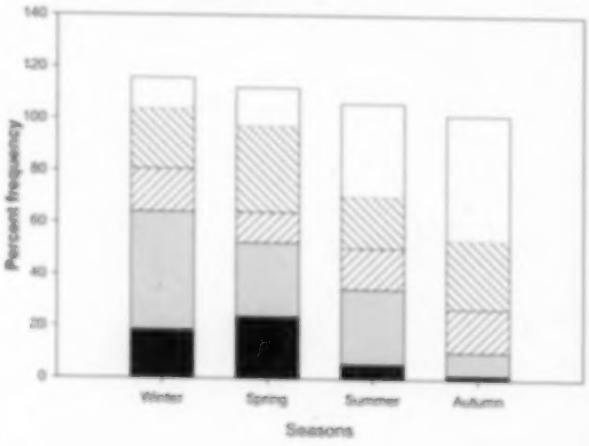
There were seasonal shifts in diet composition (Fig. 2). The highest percent occurrence of fish prey was found in the winter (16%) and spring (21%); the lowest occurrence was found during the summer (5%) and autumn (2%). The occurrence of cannibalism was high during the winter, spring, and summer (25%–39%), but decreased during the autumn (9%). The occurrence of crustaceans (10%–16%) and empty stomachs (19%–29%) were similar among all seasons. The highest occurrence of unknown prey was found in the summer (34%) and autumn (47%) samples in contrast with the low occurrence found in the spring (13%) and winter (10%). Again, the high frequency of unknown prey during summer and autumn is likely a reflection of the high number of small squid that comprised the population during these seasons and the difficulty associated with identifying their stomach contents.

Otoliths were found in ~35% of squid stomachs containing fish remains (Table 3). Overall, Myctophidae (lanternfish) were most common and constituted 30.1% of all otoliths. Although myctophids were found in squid stomachs collected during the winter and spring seasons, 87% of these were found in the spring samples. Osmeriformes (smelts–argentines) and Sternoptychidae (pearlsides) represented 18% and 8.4% of the identified otoliths, respectively, and were also consumed during the winter and spring seasons. Gadidae and Pleuronectidae together represented approximately 10% of all the otoliths. Gadids were found in stomach samples collected throughout all seasons, and pleuronectids were identified in stomach samples from every season except winter. Ammodytidae (sand lance) represented 4.2% of all otoliths collected and were identified in summer and autumn samples. Identifying fish by their otoliths is difficult at times because the size and shape may be altered during digestion. The small otoliths of juvenile fishes may also lack the distinguishing features of adult otoliths. As a result, 18.4% of otoliths were categorized as unknown. Note, however, that an unusually high number of unknown otoliths were found in the winter samples (12%). It is probable that during this season squid are consuming a group of fish for which we do not have a reference. Additionally, we collected 28 intact lower squid beaks from the diet remains; 26 were identified as *Loligo pealeii* and two were identified as *Illex illecebrosus*. We did not identify crustaceans to a lower taxonomic level; however euphausiids, and to a lesser extent hyperiid amphipods, were found in the squid stomach contents.

Table 2. Percent frequency of *Loligo pealeii* diet items and occurrence of stomachs containing single or multiple prey items.

Prey type	Frequency of occurrence
Squid, crustacean, or fish	82.56
Squid and fish	8.03
Squid and crustacean	5.14
Crustacean and fish	3.26
Squid, crustacean, and fish	1.01
Total squid	49.45
Total crustacean	27.73
Total fish	22.82

Fig. 2. Seasonal diet compositions of *Loligo pealeii* measured by percent frequency (%) of occurrence. The diet contents included fish (solid), squid (shaded), crustacean (right diagonal), empty (left diagonal), and unknown (open).



Sizes of the fish consumed by *L. pealeii* were estimated using regression equations for otolith length to total length or fork length. Regression equations were available for sand lance, *Sebastes* sp. (redfish), pearlsides, and myctophids (*Benthosema* sp.), but were not available for butterfish and cusk eel (Table 1). We were unable to identify the gadiformes to the genus or species level, but we determined the prey sizes by averaging the estimated prey body sizes calculated from regression for haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius virens*), whiting (*Merlangius merlangus*), silver hake (*Merluccius bilinearis*), and *Urophycis tenuis* (white hake) (Table 1). These species are a good representation of the Gadiformes previously reported

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Table 3. Otoliths found in *Loligo pealeii* stomach contents identified to order or family.

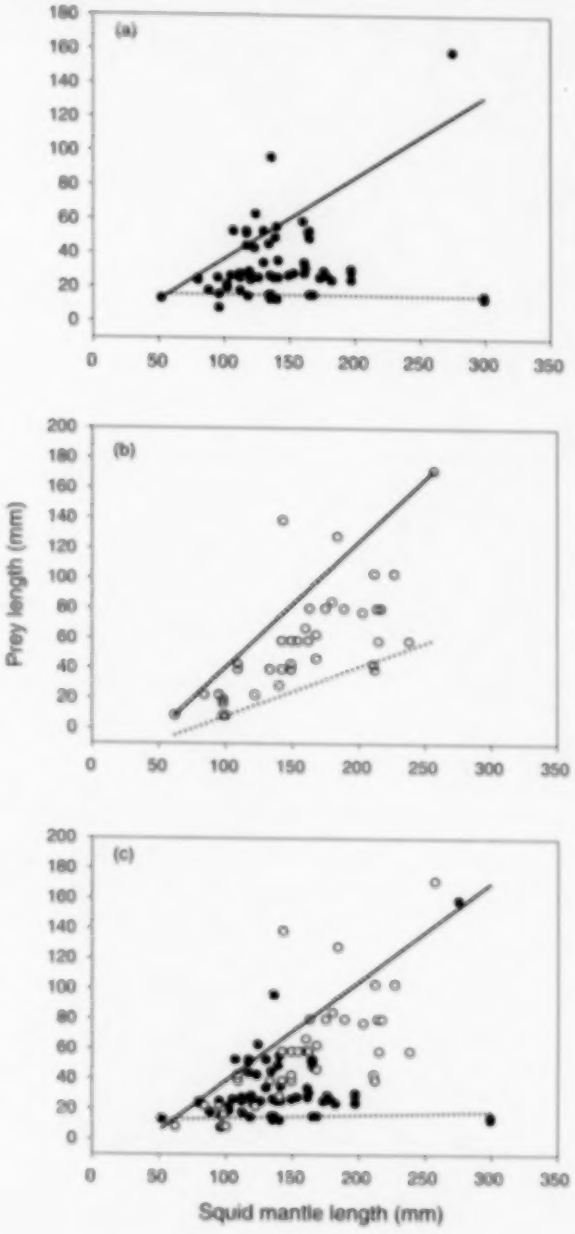
Order–Family	Winter	Spring	Summer	Autumn	Total
Myctophidae	9	61	—	—	70
Osmeriformes	3	41	—	—	44
Sternoptychidae	9	11	—	—	20
Gadiformes	6	5	2	2	15
Ammodytidae	—	—	9	1	10
Pleuronectiformes	—	4	3	2	9
Ophidiidae	—	4	2	—	6
Carangidae	—	4	—	—	4
Stromateidae	—	—	2	1	3
Sebastidae	—	2	—	—	2
Unknown	30	11	0	3	44
Broken	3	7	1	—	11
Total	60	150	19	9	238

as squid prey and (or) inhabitants of our study region during some time of the year. Additionally, the regression equations for these species were similar, providing similar estimates of prey sizes. We did not estimate the prey sizes of fish classified as Pleuronectiformes, Osmeridae, or Caraginidae because regression equations do not exist for species that well represent the order and families in our study region.

The sizes of the ingested fish ranged from 8 to 158 mm, with an average size (± standard deviation) of 32 ± 21 mm. The sizes of ingested squid ranged from 8 to 172 mm, with an average length of 58 ± 36 mm. The upper bound (90th quantile) regression of fish prey length and squid mantle length showed an increasing trend in upper prey size with predator length, although the slope was marginally nonsignificant ($p = 0.066$) (Fig. 3*a*). The lower bound (10th quantile) indicates that the lower fish prey size remained relatively constant ($p = 0.978$) (Fig. 3*a*). The quantile regression lines of the lengths of cannibalized squid indicate that maximum prey size increased with predator length ($p < 0.001$); however, in contrast with fish prey, the minimum prey size increased with predator length as well ($p = 0.002$) (Fig. 3*b*). Combining all ingested fish and squid prey, the regression lines demonstrate an increasing, though marginally nonsignificant, trend in upper prey size with increasing predator length ($p = 0.089$) and the lower prey size remained constant ($p = 0.792$) (Fig. 3*c*). Further, when we compared the upper bound regression lines of fish and squid to determine if the maximum prey size was dependent on prey type, we found no significant difference between the slopes ($p > 0.05$).

Logistic regression analyses of the stomach samples indicated a statistically significant ontogenetic shift in the diet composition of *L. pealeii* (Fig. 4). The probability of piscivory was low in small squid (<60 mm) and increased with squid size from 0.03 to 0.15 at mantle lengths between 70 and 120 mm (slope parameter ≠ 0, likelihood ratio test, 90% confidence level = 0.04, 0.07). The probability of piscivory reached approximately 0.20 in squid larger than 160 mm in length. *Loligo pealeii* were cannibalistic at all sample lengths, although there was an overall increase in cannibalism with increasing squid size. The probability of cannibalism ranged from 0.04 to 0.51, and squid were the dominant prey item

Fig. 3. Quantile regression analyses of the relationships between prey lengths (mm) and *Loligo pealeii* mantle length (mm). Solid and dotted lines represent the 90th and 10th quantiles, respectively. (*a*) Fish (solid circle); (*b*) squid (open circle); (*c*) squid and fish.



of *L. pealeii* larger than 90 mm. The probability of crustaceans being consumed by *L. pealeii* initially increased with size for small size squid (30–80 mm) and then decreased over larger squid sizes. Therefore, the logistic regression model was deemed insufficient to assess this non-monotypic trend.

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Fig. 4. Relationship between *Loligo pealeii* mantle length (mm) and the probability of piscivory (broken line) and cannibalism (solid line). Lines were estimated using logistic regression.

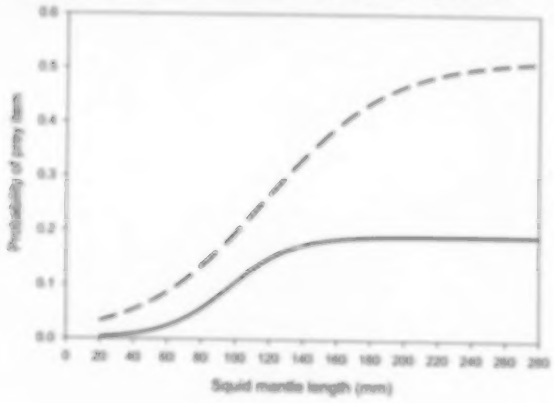
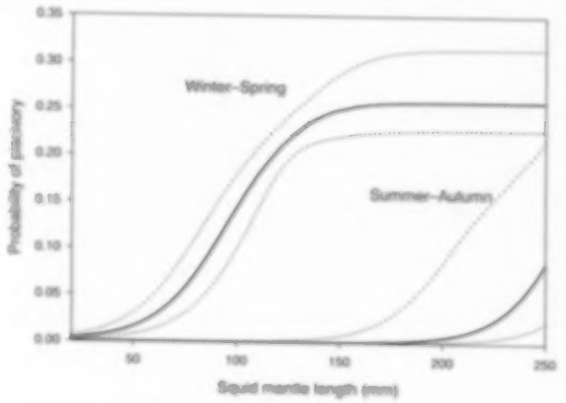


Fig. 5. Median predicted (90% prediction interval) probability of piscivory vs. body size for winter–spring samples and summer–autumn samples. The solid lines represent the medians of the likelihood distributions; dotted lines depict the 5th and 95th percentiles.



The logistic regression parameters for piscivory were significantly different between winter–spring (offshore residents) and summer–autumn (onshore residents) (Fig. 5; likelihood ratio test, $p < 0.01$). In general, squid were piscivorous at a smaller size during winter–spring. For example, the probability of piscivory of a 100 mm squid during this period was predicted to be 0.14, and 90% of the likelihood density was between 0.1 and 0.14, while during summer–autumn, the probability of piscivory was essentially 0 (Fig. 5). These contrasts in the rate of piscivory extended to the largest size classes, with 90% prediction intervals equal to 0.23–0.32 during winter–spring and 0.02–0.22 during summer–autumn (Fig. 5).

To evaluate whether the seasonal patterns of piscivory may be explained by prey size constraints, we coupled the size distributions of our squid samples with our quantile regression results and published estimates of juvenile fish body sizes. Our analyses only included juvenile fish that are known to spatially overlap with *L. pealeii* as evidenced by squid sampling locations (Fig. 1) and previous literature documenting seasonal spatial distributions of mid-Atlantic fish species. *Loligo pealeii* shared similar habitats with various commercial fish species throughout the year (Table 4), as well as with cusk eels and mesopelagic fish, including myctophids and sternoptychids (Bigelow et al. 1964; Sherman et al. 1984; Able and Fahay 1998).

The results of our analyses showed that in February the squid population was composed of larger individuals, and a high number of juvenile fish species fell within the prey size spectra of the *L. pealeii* population (Fig. 6*a*). The length distribution of the squid population in March was fairly homogeneous, and again, there were a high number of juvenile fish species vulnerable to predation by squid of all sizes (Fig. 6*b*). In June, the squid population was dominated by smaller squid, and a high number age-0 fish were of appropriate prey sizes for almost all lengths of *L. pealeii* (Fig. 6*c*). In September, the squid population was again dominated by small individuals; however, the availability of juvenile fish of suitable prey sizes was low for the majority of the population (Fig. 6*d*). Only large squid (>200 mm) were capable of consuming high numbers of juvenile fish species during this period.

Discussion

Our analyses produced three main findings. First, predation on fish and squid by *L. pealeii* were dictated by size-related constraints, such that the prey size spectrum was a function of increasing predator size. Second, there were pronounced seasonal shifts in the frequency of piscivory among *L. pealeii*. The incidence of piscivory was higher in winter–spring than during summer–autumn. Third, there were seasonal shifts in the ontogenetic onset of piscivory, evidenced by small size-at-piscivory during winter–spring compared with summer–autumn. These findings suggest that variation in the frequency and intensity of piscivory are related to shifts in the size structures of both *L. pealeii* and prey populations. We describe the potential mechanistic linkages among our three main findings in detail below.

Estimates of *L. pealeii* prey sizes showed an increasing trend in the prey size spectra over increasing squid mantle lengths, consistent with previous studies documenting the prey sizes of squid (Rocha et al. 1994; Collins and Pierce 1996; Phillips et al. 2003). The increased range of the prey size spectrum with body size was largely governed by an increase in the upper bound of the spectrum (i.e., the maximum-sized prey increased with increasing squid size and lowest-sized prey remained fairly constant). This increase in prey size with predator size is consistent with the observation of more diverse food habits as squid become larger (Vovk 1985; Collins et al. 1994; Pierce et al. 1994). In general, diets of small squid are dominated by crustaceans, while diets of larger squid consist of many species of fish, squid, and crustacean.

Size constraints on feeding can explain our observation that the frequency of piscivory was greatest during the winter and spring. We hypothesize that the high incidence of piscivory in winter–spring was due to the joint effects of large *L. pealeii* body sizes and the availability of many suit-

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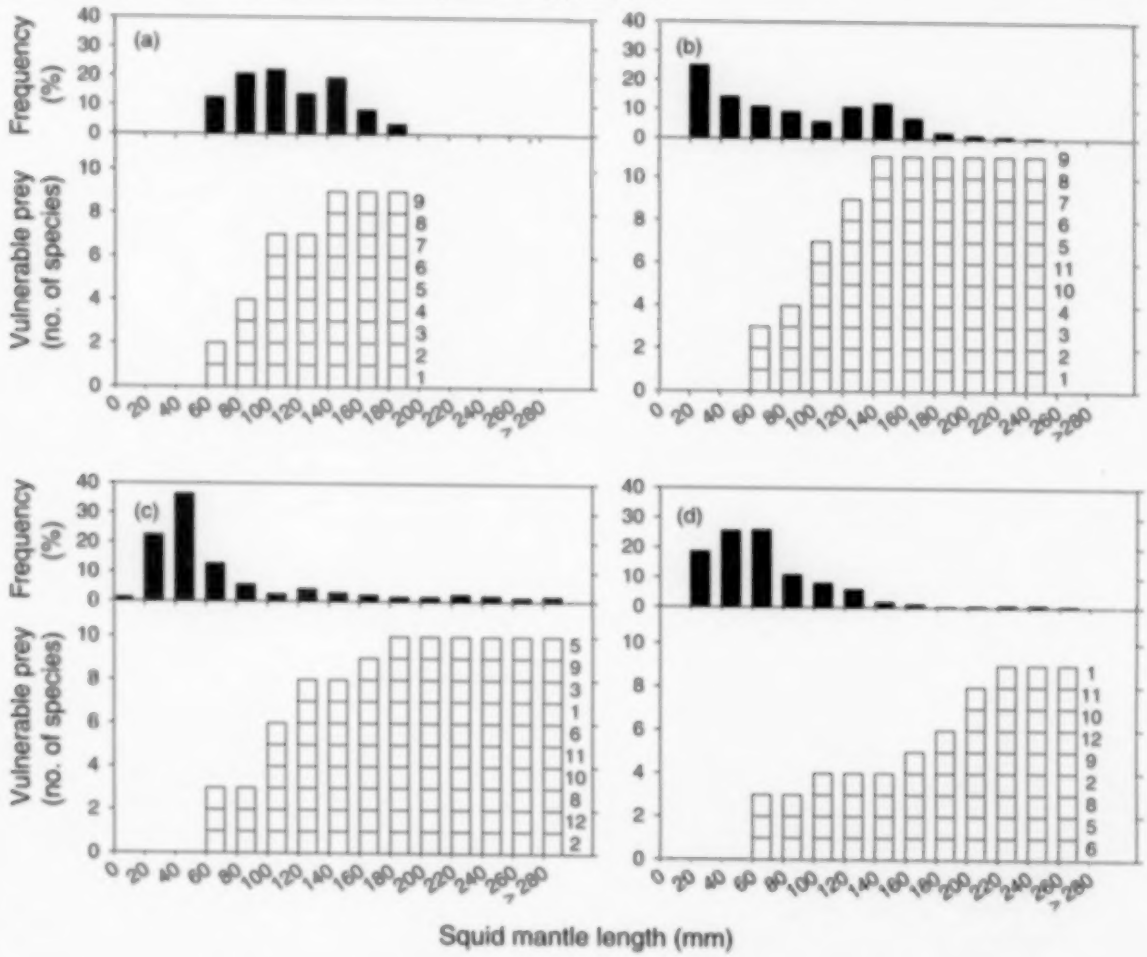
Table 4. Seasons of potential spatial overlap between *Loligo pealeii* collected on National Marine Fisheries Service (NMFS) seasonal trawl surveys and larval–juvenile commercial fish.

Fish species	Seasons	Reference
Gadiformes		
Merluccius bilinearis	W, Sp, S, A	Vovk 1974; Sherman et al. 1984; Lock and Packer 2004
Melanogrammus aeglefinus	Sp, S, A	Sherman et al. 1984; Cargnelli et al. 1999*a*
Pollachius virens	W, Sp, S, A	Able and Fahay 1998; Cargnelli et al. 1999*b*
Urophycis sp.	W, Sp, S, A	Able and Fahay 1998; Chang et al. 1999*a*; Steimle et al. 1999
Pleuronectiformes		
Paralichthys dentatus	W, Sp, S, A	Able et al. 1989; Able and Fahay 1998; Packer et al. 1999
Scophthalamus aquosus	Sp, S, A	Sherman et al. 1984; Morse and Able 1995; Chang et al. 1999*b*
Peprilus tricanthus	W, Sp, S, A	Sherman et al. 1984; Able and Fahay 1998; Cross et al. 1999

Note: W, winter; Sp, spring; S, summer; A, autumn.

Fig. 6. Size distributions of *Loligo pealeii* (top panels) and the number of juvenile fish species vulnerable to predation by squid based on size constraints (bottom panels), calculated for (*a*) February, (*b*) March, (*c*) June, and (*d*) September. Juvenile fish (with number codes in parentheses) include pollock (*Pollachius virens*) (1); summer flounder (*Paralichthys dentatus*) (2); spotted hake (*Urophycis regia*) (3); Myctophids (*Benthosema* sp.) (4); silver hake (*Merluccius bilinearis*) (5); red hake (*Urophycis chuss*) (6); sternoptychids (Sternoptychidae) (7); butterfish (*Peprilus tricanthus*) (8); cusk eel (Ophidiidae) (9); white hake (*Urophycis tenuis*) (10); windowpane (*Scophthalmus aquosus*) (11); and haddock (*Melanogrammus aeglefinus*) (12).



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ably sized fish. Squid larger than 120 mm were relatively common during this time period, but were rare during summer–autumn. These shifts were likely due to the seasonal pattern of growth and reproduction that produces large numbers of juveniles in the summer and early autumn, which then grow rapidly until they reach maturity and die (<1 year; Brodziak and Macy 1996; Macy and Brodziak 2001). The availability of fish prey was partly enhanced by the offshore movement of squid during the winter and early spring (Summers 1969; Serchuk and Rathjen 1974), which exposed them to small mesopelagic fish, such as myctophids and sternopytchids (Rodhouse and Nigmatullin 1996). In addition, numerous neritic fish species spawn and produce small-sized larvae and juveniles during this time period (Sherman et al. 1984).

Size constraints on feeding were also consistent with our observation that the onset of piscivory shifted throughout the year. In general, squid were piscivorous at much smaller body sizes during the winter–spring than during summer–autumn. For instance, 20% of the 125 mm squid in the winter–spring were predicted to be piscivorous, but essentially none of the same-sized squid in the summer–autumn were piscivorous. Based on our estimates of juvenile fish growth rates, we identified 9 species whose adult or juvenile body sizes would be vulnerable to a 125 mm squid during spring. In contrast, only four species had juveniles that were within the prey size spectrum of a 125 mm squid during autumn. These contrasts were partly due to juveniles outgrowing the prey size spectrum of *L. pealeii*, but also due to seasonal shifts in the spatial overlap of squid with smaller-bodied prey such as myctophids. Thus, we concluded that the estimated prey size spectrum of *L. pealeii* and available prey body sizes are consistent with the hypothesis that size constraints governed the seasonal variation in the onset of piscivory.

Size-structured interactions between squid and their prey may impact the recruitment success of larval and juvenile fish. The extent of this impact depends on the variability of the factors dictating size-based interactions, including predator and prey growth rates and size distributions and the strength of spatiotemporal overlaps between predators and prey (Rice et al. 1997). For example, at some point during the summer, the squid population shifts from being heterogeneous to being largely composed of small individuals. This shift is likely a result of the recruitment of larval–juvenile squid from the spring–summer spawning period and the loss of many adults to post-spawning mortality. Importantly, the timing of this shift in size structure may govern the intensity of piscivory during the summer and potentially the recruitment success of larval and juvenile fish. If squid spawn early in the season, the population will be composed of mostly small squid, and predation rates will be low, since juvenile fish will be too large to be consumed by the majority of the population. However, if peak spawning occurs later in the season, the squid population may be more heterogeneous in size, and the predatory impact on juvenile fish may be much greater. The degree of spatial overlap between *L. pealeii* and juvenile fish will also determine the impact of these size-structured interactions. Comparisons among our sampling sites and previously documented fish distributions revealed the potential for strong spatial overlaps between *L. pealeii* and multiple fish species, including commercially valuable fish such as gadiformes and pleuronectiformes. The strength of these overlaps may have the most impact on fish populations during the winter–spring months when the occurrence of piscivory appears to be highest. Determining the degree and variability of these spatiotemporal overlaps is beyond the scope of our study; however, these factors will affect the strength of predator–prey interactions and should be a focus of future studies.

Understanding size-structured interactions and the factors governing these interactions is critical for determining the predatory impact of squid on fish populations. This knowledge is especially valuable for quantifying squid predation on over-harvested fish populations. Increased periods of predation on larval–juvenile stages of these populations may impede recruitment success, potentially leading to depensatory effects. To evaluate the potential for recruitment limitations, better estimates of squid predation on fish, and in particular on over-harvested fish species, are needed. Our estimates of piscivory are low in comparison with past studies (Vinogradov and Noskov 1979; Maurer and Bowman 1985; Vovk 1985), which may be attributed to the limitations of gut content analyses. First, squid macerate their prey and tend to discard the heads and hard parts of fish during feeding (Nixon 1987; Dawe et al. 1997). In particular, squid are more likely to discard the heads of larger fish (Rodhouse et al. 1992; Pierce et al. 1994; Dawe et al. 1997). Second, squid have high digestion rates (Bidder 1950), thus prey that have been consumed may not be detected in the stomach contents. As a consequence, it is difficult to quantify the percent diet composition of squid (by mass or number), and estimates of percent frequency of occurrence are likely to be underestimated. However, size relations are more robust to the limitations of gut content analyses because only observed prey sizes are used to draw conclusions regarding prey size constraints. Studies aiming to quantify the percent diet composition of squid may benefit from coupling gut content analyses with stable isotope or fatty acid analyses.

Few otoliths were collected from the diets of larger squid (>200 mm) in this study, which was most likely a result of squid feeding behavior. Although, the absence of otoliths may also be due to the overall low sample size of large squid (>200 mm), comprising only 12% of the total sample set. Our estimates of maximum prey sizes for *L. pealeii* were somewhat imprecise because of the low number of prey sizes identified for larger squid, which may further explain the marginally nonsignificant slope of upper prey sizes for fish and combined prey.

In summary, analyses of *L. pealeii* prey size spectra and the size distributions of squid and their potential prey provide support for the notion that size constraints dictate the patterns of piscivory. The squid population was composed of large, summer-spawned individuals during the winter–spring, and there were a high number of juvenile fish species that fell within the prey size spectrum of the squid population. In contrast, the summer – early autumn squid population was dominated by larval–juvenile squid, and the number of vulnerable prey species available to *L. pealeii* decreased within this period. Consequently, the ecological interactions between squid and fish may vary critically throughout the year, where *L. pealeii* acts as an important predator during winter

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and spring, but acts largely as a prey species for fish in the summer and early autumn.

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Effects of low-head barriers on stream fishes: taxonomic affiliations and morphological correlates of sensitive species

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Abstract: Low-head barriers used in the control of parasitic sea lamprey (*Petromyzon marinus*) in the basin of the Laurentian Great Lakes can alter the richness and composition of nontarget fishes in tributary streams. Identification of taxa sensitive to these barriers is an important step toward mitigating these effects. Upstream–downstream distributions of fishes in 24 pairs of barrier and reference streams from throughout the basin were estimated using electrofishing surveys. For 48 common species from 34 genera and 12 taxonomic families, 8–19 species, 5–16 genera, and 2–7 families showed evidence of being sensitive to barriers, with the variation in number depending on the statistical measure applied. Barriers did not differentially affect species from certain genera or families, nor did they affect species of certain body form. Therefore, taxonomic affiliation and swimming morphology are not useful for predicting sensitivity to barriers for fishes that co-occurred with sea lampreys but were not sampled adequately by our survey. Our estimates of sensitivity will help fisheries managers make sound, defensible decisions regarding the construction, modification (for fish passage), and removal of small, in-stream barriers.

Résumé : Les barrières de faible hauteur utilisées pour le contrôle de la grande lamproie marine (*Petromyzon marinus*) parasite dans le bassin versant des Grands Lacs laurentiens peuvent modifier la richesse et la composition des peuplements de poissons non ciblées dans les cours d'eau tributaires. L'identification des taxons vulnérables à la présence de ces barrières est une étape importante vers la mitigation de ces effets. Des inventaires à la pêche électrique nous ont servi à estimer la répartition amont–aval des poissons dans 24 paires de cours d'eau (l'un avec barrière, le second servant de témoin) répartis dans l'ensemble du bassin. Sur un total de 48 espèces communes appartenant à 34 genres et 12 familles taxonomiques, 8–19 espèces, 5–16 genres et 2–7 familles montrent une sensibilité aux barrières; la variation des nombres dépend de la mesure statistique utilisée. Les barrières n'affectent pas de façon différente les espèces de certains genres ou familles ou d'une forme de corps particulière. Ainsi, l'affiliation taxonomique et la morphologie reliée à la nage ne sont pas des variables utiles pour prédire la sensibilité aux barrières chez les poissons qui cohabitent avec la grande lamproie et qui n'ont pas été échantillonnés adéquatement dans notre inventaire. Nos estimations de sensibilité vont aider les gestionnaires de la pêche à arriver à des décisions solides et défendables au sujet de la construction, de la modification (pour laisser passer les poissons) et l'élimination des petites barrières érigées dans les cours d'eau.

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Introduction

Despite considerable interest in the effects of human actions on the environment, identifying species sensitive to specific actions remains an important and challenging research problem. The problem is important for identifying species that may be influenced by future actions, prioritizing species for research into ways of mitigating effects, developing policies aimed at minimizing unwanted effects, and identifying species to monitor in conservation or restoration plans. The problem is challenging because in many situations the number of species to be considered is high. It is also challenging because pertinent, related, but different concepts with fuzzy definitions, such as indicator species, sensitive species, vulnerable species, and sentinel species, have been described using similar terminology (Gibbons and Munkittrick 1994; Simberloff 1998; Caro and O'Doherty 1999). It is challenging further because there is no consensus on how to demonstrate sensitivity. Initial methods for identifying sensitive taxa vary in their selection criteria and conceptual approach and have not always been validated adequately (Jones and Kaly 1996; Power and McCarty 1997). More rigorous methods are still being developed and assessed and may require significant amounts of data and data collection effort (Hewitt et al. 2001; Stewart-Oaten and Bence 2001).

Small dams and in-stream barriers represent one of the most common human alterations of the North American waterscape (Graf et al. 2002; Poff and Hart 2002; Graf 2003). From a biological perspective, these structures are becoming a source of heightened concern because of their potential to restrict movements of fishes and to fragment streams and rivers (Jungwirth et al. 1998). For similar reasons, they are also becoming an attractive, potential tool for ecosystem management because they can restrict the movements of invasive species, thereby protecting native species and ecosystems (Bergstedt and Holmes 1997; Sharov and Liebhold 1998; Stokstad 2003). Greater information on the effects of these structures is needed to help fisheries and aquatic managers make sound, defensible decisions regarding the construction, modification (for fish passage), and removal of these structures.

We evaluate the sensitivity of fish species to the presence of low-head, in-stream barriers used in the biological control of sea lamprey (*Petromyzon marinus*) in the Laurentian Great Lakes. The sea lamprey is a parasitic fish that feeds on the blood and tissue of other large fishes (hosts). Its origin in Lake Ontario is uncertain, but it invaded Lakes Erie, Huron, Michigan, and Superior during the construction of shipping passages in the 1920s. Subsequently, this non-native species, combined with commercial fishing and habitat change, had strong detrimental effects on populations of large native fishes, such as lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), burbot (*Lota lota*), and suckers (*Catostomus* spp.) (Smith 1968; Henderson 1986; Liu and Jensen 1992). Since the late 1950s, sea lampreys have been controlled successfully by periodically treating larval-rearing habitat in streams with the lampricide 3-trifluromethyl-4-nitrophenol (TFM). The agency that directs the control program is the Great Lakes Fishery Commission (GLFC). The GLFC recently pledged to reduce its reliance on TFM in response to growing public concern regarding introduction of chemicals into the environment and to increasing costs of TFM (GLFC 1992, 2001). Low-head barriers (~0.4–2.0 m in height) are an attractive, alternative control method. They deny maturing sea lampreys access to spawning habitat in streams, reduce the amount of stream treated with TFM, and reduce the exposure of nontarget fishes to lampricide. However, evaluations of the effects of these barriers on nontarget fishes are just beginning.

We evaluate sensitivity by comparing the relative abundances of fish species, genera, and taxonomic families above and below a barrier on a stream with their relative abundances above and below a hypothetical barrier on a corresponding reference stream. We first use field survey data to assess sensitivity for a set of common fish taxa using three statistical measures differing in the information used and assumptions made. We then examine whether species from the same genera or family tend to exhibit a similar level of sensitivity to barriers. Following this, we examine whether morphological correlates of swimming ability and use of fast-flowing water provide good predictors of the measures of sensitivity. Taxonomic affiliation and morphology are examined because these attributes may be useful for predicting the sensitivity of fishes found in streams that produce sea lamprey within the basin but not sampled adequately in our field survey. Sensitivity to barriers is assessed at the levels of species, genus, and taxonomic family because local population declines can be nonrandom within taxa (Purvis et al. 2000) and because patterns that are variable or noisy at the species level may be more apparent at higher taxonomic levels (Rodríguez and Lewis 1997).

The findings presented here are part of a larger, extensive research program examining the basin-wide effects of low-head barriers on fishes other than the sea lamprey. Earlier papers demonstrated that barriers alter the longitudinal decline in species richness within streams (Dodd et al. 2003; Hayes et al. 2003) and restrict the movements of common fishes (Porto et al. 1999).

Materials and methods

Design of field surveys

Twenty-four stream pairs, made up of 47 streams from across the basin of the Laurentian Great Lakes, were surveyed in the summer of 1996. Each pair consisted of a barrier stream with a low-head, sea lamprey barrier and a corresponding reference stream without a low-head, sea lamprey barrier. One reference stream had to be used in two pairs. We refer to streams lacking a sea lamprey barrier as references, rather than controls, to acknowledge that our study was not an experiment where barriers were assigned at random to streams within each pair. Stream selection and pairing were made in consultation with control agents and technical experts from Fisheries and Oceans Canada and US Fish and Wildlife Service. All streams had a history of producing sea lamprey. Streams within pairs were matched for geographical proximity and their general geology, size, flow, habitat characteristics, and, therefore, likelihood of supporting similar fish assemblages. Post hoc analyses demonstrated that barrier and reference streams did not differ systematically in catchment area, land cover (percentages of forest,

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agricultural, and urban cover), and surficial geology (percentages of glacial, lacustrine, and outwash deposits and bedrock) (multivariate analysis of variance: F test comparing barrier and reference streams after blocking by stream pair = 0.71, df = 7,17, $P > 0.60$). Streams within pairs were deliberately not matched based on information about fish assemblages because such overmatching could obscure any effects a low-head barrier might have had on fishes. Information on the physical characteristics of the sample sites is provided in Dodd et al. (2003).

For each reference stream, a hypothetical barrier location was selected to correspond with the barrier location (distance from the stream mouth) on the paired barrier stream. Six stream sections, three above the barrier or hypothetical barrier and three below, were then surveyed for most streams. Each stream survey section was five to seven times the wetted stream width. Survey sections were separated by stream sections of at least five times stream width and typically longer depending on the availability of access points. The size and separation of stream sections were based on advice from the literature (Simonson and Lyons 1995) and from control agents and technical experts who were familiar with the streams. Survey sections closest to the barrier locations were selected so as not to include any small reservoir above the barrier or any plunge pool below the barrier. This was done to focus on detection of larger scale effects beyond the immediate vicinity of the barriers. On one stream, the barrier was too close to the stream mouth for us to survey three stream sections below the barrier. In this instance, we surveyed the entire downstream section.

Fishes within each stream section were sampled by single-pass, backpack electrofishing in the upstream direction (Dodd et al. 2003). Captured fish were identified to species and measured (total length in mm). Voucher specimens of fishes that could not be identified in the field were sacrificed with tricaine methane sulfonate (MS-222), fixed in 10% formalin, preserved in 70% ethanol, and later identified by us or by T. Coon (Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA) or E. Holm (Centre for Biodiversity and Conservation Biology, Royal Ontario Museum, Toronto, ON M5S 2C6). Voucher specimens were deposited in the Royal Ontario Museum.

Assessment of sensitivity to barriers

For each fish taxon, our survey data provided estimates of relative abundance above and below a low-head barrier on a barrier stream and for corresponding locations on the paired reference stream (Appendix A). Three statistical measures were used to assess sensitivity to barriers for every taxon where adequate data were obtained to make the calculations. Each measure compared estimates of a taxon's abundance above and below barriers against estimates of the taxon's abundance above and below hypothetical barrier locations on reference streams, because longitudinal distributions of taxa vary naturally within streams (Vannote et al. 1980; Matthews 1998). The first measure was an odds ratio (OR)

$$(1) \qquad \mathrm{OR} = (a/b)/(c/d)$$

where a was the number of individuals of that taxon (species, genus, or family) collected above the barrier location for the 24 barrier streams, b was the number collected below the barrier location, c was the number collected above the hypothetical barrier location for the 23 reference streams, and d was the number collected below the hypothetical barrier location. OR < 1 indicates that a species' abundance above barriers relative to below on barrier streams is less than that expected based on the abundances observed for reference streams. Values greater than 1 indicate the species abundance above versus below barriers is greater than expected based on reference streams. For each OR, exact 95% confidence limits were calculated using the method of Sterne (1954).

The second measure was a common odds ratio (OR_c) obtained when a, b, c, and d were stratified by stream pair (Breslow and Day 1980). OR_c only considers stream pairs (strata) where individuals of a given taxon were observed in sample sections above and below a barrier location for either stream within the pair (i.e., $a + c > 0$ and $b + d > 0$) and observed in both barrier and reference streams ($a + b > 0$ and $c + d > 0$). OR_c was calculated because the direction of the association quantified by the OR and the corresponding interpretation can be altered when data from strata are combined to form a single group, owing to differential weighting of the strata (Simpson's paradox) (Mittal 1991; Moore and McCabe 1999). Interpretation of OR_c is the same as that for the OR above. For each OR_c, exact 95% confidence limits were calculated using the method of Sterne (1954).

The third measure, the ratio of catch per unit effort (CPUE), was calculated using generalized linear models with Poisson error distributions (McCullagh and Nelder 1989). The ratio of CPUE was calculated to provide a measure that was comparable with the OR measures, but accommodated variation in sampling effort among streams and among locations above and below barrier locations. A Poisson error distribution was assumed because our abundance measurements were counts with values ≥0 and the distributions of values were skewed. The number of individuals from a given taxon collected in a given survey area can be represented as

$$(2) \qquad N_{ijk} = c_{ijk}\, t_{ijk}$$

where N_{ijk} is the number captured, c_{ijk} is the CPUE, and t_{ijk} the effort in electroshocking time (s) in stream pair i, stream type j (barrier or reference), and location k relative to the barrier (above or below). Log transformation provides the additive model

$$(3) \qquad \log(N_{ijk}) = \log(c_{ijk}) + \log(t_{ijk})$$

The analyses modeled $\log(N_{ijk})$ with stream pair, barrier type, location relative to the barrier, and the statistical interaction between barrier type and location relative to the barrier as explanatory variables, with $\log(t_{ijk})$ to compensate for variation in sampling effort. The interaction coefficient provided a CPUE ratio, log-transformed, that was directly analogous to the ORs above. Overall, goodness-of-fit statistics indicated that the models had variances greater than that expected for a Poisson distribution (overdispersion). Following McCullagh and Nelder (1989), overdispersion was accommodated by adding a dispersion parameter estimated as the goodness-of-fit χ^2 divided by the model degrees of freedom. This dispersion parameter does not affect the estimate of the CPUE ratio, but does influence the standard error of the esti-

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mate. 95% confidence limits for the CPUE ratio were calculated using likelihood ratios. Values of CPUE ratio were back-transformed to make them comparable with the values of the corresponding ORs. Analyses using sampling area as the measure effort provided estimates of the CPUE ratio that were very similar to those obtained when using sampling time (R. McLaughlin, unpublished data).

Taxonomic affiliation and sensitivity

Relationships between taxonomic affiliation and sensitivity were assessed using intraclass correlations, which provide an estimate of the power of one species to predict the sensitivity of another species within the same group (e.g., family or genus within family) (Harvey and Pagel 1991). Intraclass correlations were calculated using variance components estimated from nested analyses of variance considering family and genus within family as random effects. The specific variance components were estimated using restricted maximum likelihood, which is recommended over least-squares because it guards against negative estimates of the variance components and is better suited for unbalanced designs (Searle et al. 1992). A normal deviates transformation (Legendre and Legendre 1998) was applied to the values of the OR and OR_c prior to analysis. The values were transformed because the ORs had skewed distributions ranging from 0 to ∞ and because the transformations helped normalize the distributions of residuals and equalize the variances among genera and families. The transformation entailed ranking the OR values, selecting and ranking an equal number of random normal deviates, and assigning each ranked normal deviate to the corresponding ranked OR value. In the case of tied OR values, the assignment of a normal deviate was made randomly. The CPUE ratio was log-transformed back to its original scale of measurement prior to analysis.

Morphology and sensitivity

Geometric mean fork lengths were calculated for all species collected in our field survey. It was not feasible to measure body shapes of field specimens because of the time required to sample fishes and habitat features (Dodd et al. 2003) at all 47 streams in the same field season. Therefore, drawings from Trautman (1981) were digitized for 39 of the species for which we estimated sensitivity and six morphological attributes were measured using the National Institutes of Health (NIH) Image program (Version 1.61; available from http://rsb.info.nih.gov/nih-image/). The attributes were total length, body depth, minimum caudal peduncle depth, caudal peduncle length, caudal fin length, and caudal fin span, as defined by Trautman (1981). Total length (mm) was measured from the most anterior point of the upper snout to the furthest tip of the caudal fin. For each species, the total length of specimens used for the drawings was also provided by Trautman (1981) and used to calibrate all measurements taken. Body depth was the greatest vertical distance from the dorsal to the ventral body surface exclusive of fleshy or scaly structures connected with the fin bases. Minimum caudal peduncle depth was the smallest distance in a straight line from the midline of the dorsal surface of the caudal peduncle to the midline of the ventral surface. Caudal peduncle length was the oblique distance from the insertion of the anal fin base to the caudal fin base. Caudal fin length was the distance from the most anterior point of caudal fin to the most posterior point. Caudal fin span was the distance from the most dorsal point of caudal fin to the most ventral point when the fin is spread open. When images of adult male and female individuals were provided, both diagrams were measured and averaged for analysis. The measured attributes were selected as predictors of general locomotor performance and use of challenging flow conditions based on earlier theoretical (Webb 1984, 1988) and empirical (e.g., Taylor and McPhail 1985; Bisson et al. 1988; Matthews 1998) treatments linking morphology with swimming performance and habitat use. We opted for this general approach because of uncertainty regarding how the fishes respond to barriers. Most species of stocked Pacific salmon (*Oncorhynchus* spp.) can jump over the barriers (Kelso and Noltie 1990), but jumping abilities of fishes native to the Great Lakes are poorly known, and it is commonly believed that native fishes traverse small barriers at times when the barriers are inundated (e.g., Cumming 2004).

Trautman's (1981) drawings were considered adequate for our analyses based on five criteria. First, our analyses focused on the coarse size and shape variation among species. Second, Trautman drew individuals considered to be representative of a given species based on 20–40 morphological measurements, depending on the species, made from 10–50 individuals of various sizes (Trautman 1981). Third, mean fork lengths ($\log_{10}$-transformed) of the specimens collected in our study were correlated reasonably strongly with the total lengths ($\log_{10}$-transformed) from Trautman ($r = 0.73$, $P < 0.0001$, $n = 39$ species). Fourth, for the species considered in our analysis, body depths (35 species), caudal peduncle depths (12 species), and caudal peduncle lengths (four species), expressed as percentages of total length, were consistent with corresponding estimates provided in Scott and Crossman (1973). Finally, morphological measurements were made for a single preserved specimen from each of 12 species. The specimens were obtained from the fish collection housed at the University of Guelph. After adjusting statistically for differences in total length, the relative sizes of the morphological features were significantly correlated between the specimens in Trautman's drawings and the specimens we measured ($r = 0.99$, 0.96, 0.70, 0.68, and 0.69 for body depth, minimum caudal peduncle depth, caudal peduncle length, caudal fin length, and caudal fin span, respectively; all with $P < 0.02$). For a fish 129 mm in total length, mean sizes of measurements made from the drawings and from the preserved specimens, respectively, were 26 and 26 mm for maximum body depth, 11 and 12 mm for minimum caudal peduncle depth, 18 and 18 mm for caudal peduncle length, 24 and 24 mm for caudal fin length, and 25 mm and 27 for caudal fin span.

Our measures of sensitivity were correlated with both univariate and multivariate measures of size and shape using Kendall's rank correlations. In univariate analyses, the morphological measures were $\log_{10}$-transformed. Fork length was then used as a measure of size, and the remaining morphological (shape) measures were adjusted for size using the allometric method of Reist (1986). In the multivariate analyses, a principal components (PC) analysis conducted on the

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Table 1. Identification of species sensitive to low-head barriers based on the catch-per-unit-effort (CPUE) ratio, odds ratio (OR), and common odds ratio (OR_c).

Common name	Scientific name	CPUE ratio	OR	OR_c	Occurrence	
					One stream of a pair	Both streams of pair
Striped shiner	*Luxilus chrysocephalus*	0 (0 – >999)	0 (0–6.65)	—	2	0
Northern redbelly dace	*Phoxinus eos*	**0** (0–0.19)	**0** (0–0.11)	**0** (0–0.46)	10	2
Iowa darter	*Etheostoma exile*	0 (0 – >999)	0 (0–4.99)	—	3	0
Sea lamprey	*Petromyzon marinus*	**0** (0–0.26)	**0** (0–0.48)	**0** (0–0.69)	11	3
Yellow perch	*Perca flavescens*	0 (0–1.20)	**0** (0–0.68)	**0** (0–0.52)	9	2
Trout-perch	*Percopsis omiscomaycus*	0 (0–4.96)	0 (0–8.06)	0 (0–29.0)	4	1
Fathead minnow	*Pimephales promelas*	**0.02** (0.00–0.20)	**0.02** (0–0.16)	**0.07** (0–0.79)	9	2
Northern pike	*Esox lucius*	**0.05** (0–0.45)	**0.05** (0.01–0.41)	0 (0–4.99)	9	1
Logperch	*Percina caprodes*	**0.09** (0.01–0.43)	**0.09** (0.03–0.26)	**0.05** (0–0.23)	17	7
Pearl dace	*Margariscus margarita*	0.14 (0–11.6)	0.14 (0.01–1.31)	—	6	0
Fallfish	*Semotilus corporalis*	0.17 (0.01–2.33)	0.17 (0.01–3.17)	0.17 (0.01–3.17)	1	1
Northern hog sucker	*Hypentelium nigricans*	0.19 (0–423)	0.19 (0.01–2.60)	0.67 (0.01–11.6)	3	2
Largemouth bass	*Micropterus salmoides*	0.19 (0–11.1)	0.19 (0.01–2.28)	0.11 (0.00–3.19)	4	1
Cutlip minnow	*Exoglossum maxillingua*	**0.24** (0.07–0.74)	**0.24** (0.07–0.82)	**0.24** (0.07–0.82)	1	1
Central mudminnow	*Umbra limi*	0.27 (0.05–1.18)	**0.27** (0.17–0.43)	1.45 (0.76–3.20)	19	12
Common carp	*Cyprinus carpio*	0.39 (0.01–20.4)	0.39 (0.09–1.73)	1.80 (0.15–94.19)	5	2
Longnose dace	*Rhinichthys cataractae*	0.44 (0.18–1.03)	**0.44** (0.37–0.52)	**0.82** (0.63–0.97)	23	16
Brook stickleback	*Culaea inconstans*	0.47 (0.06–2.48)	0.47 (0.21–1.02)	**0.28** (0.07–0.92)	17	4
Rosyface shiner	*Notropis rubellus*	0.58 (0–28.8)	0.58 (0.21–1.63)	—	4	0
American brook lamprey	*Lampetra appendix*	0.69 (0.03–12.7)	0.69 (0.23–2.13)	**10.5** (1.09–254)	6	1
Rock bass	*Ambloplites rupestris*	0.70 (0.29–1.72)	0.70 (0.45–1.11)	**0.36** (0.16–0.59)	22	10
Coho salmon	*Oncorhynchus kisutch*	0.73 (0 – >999)	0.73 (0.16–3.61)	—	4	0
Mottled sculpin	*Cottus bairdii*	0.80 (0.35–1.82)	**0.80** (0.67–0.96)	**0.80** (0.60–0.94)	21	17
White sucker	*Catostomus commersoni*	0.83 (0.36–1.92)	0.83 (0.56–1.22)	**0.60** (0.35–0.99)	22	16
Common shiner	*Luxilus cornutus*	0.87 (0.28–2.67)	0.87 (0.62–1.24)	**0.45** (0.24–0.72)	16	10
Smallmouth bass	*Micropterus dolomieu*	0.89 (0.07–27.2)	0.89 (0.15–7.19)	>999 (0.14 – >999)	8	1
Blacknose dace[a]	*Rhinichthys atratulus*	0.98 (0.46–2.08)	0.98 (0.83–1.16)	**1.35** (1.16–1.73)	22	15
Rainbow darter	*Etheostoma caeruleum*	1.00 (0.13–6.91)	1.00 (0.53–1.83)	1.02 (0.55–1.91)	2	2
Stonecat	*Noturus flavus*	1.10 (0.01–210)	1.10 (0.10–11.9)	—	4	0
Creek chub	*Semotilus atromaculatus*	1.13 (0.49–2.59)	1.13 (0.89–1.43)	**1.5** (1.22–2.25)	23	17
Johnny darter	*Etheostoma nigrum*	1.22 (0.51–2.94)	1.22 (0.91–1.63)	**1.91** (1.45–3.30)	22	15
Pumpkinseed	*Lepomis gibbosus*	1.23 (0.08–34.5)	1.23 (0.36–4.07)	0.02 (0.00–1.33)	15	3
Blackside darter	*Percina maculata*	1.23 (0.07–53.8)	1.23 (0.32–4.83)	2.18 (0.43–24.2)	9	2
Rainbow trout	*Oncorhynchus mykiss*	1.27 (0.50–3.26)	**1.27** (1.02–1.58)	**1.38** (1.02–2.05)	21	16
Bluntnose minnow	*Pimephales notatus*	1.39 (0.18–20.9)	1.39 (0.46–4.34)	>999 (0.75 – >999)	12	1
Brown trout	*Salmo trutta*	1.70 (0.02–412)	1.70 (0.66–4.38)	1.80 (0.29–15.3)	13	2
Fantail darter	*Etheostoma flabellare*	1.85 (0.45–8.63)	**1.85** (1.18–2.88)	**2.49** (1.56–4.07)	4	3
Hornyhead chub	*Nocomis biguttatus*	2.45 (0.56–12.1)	**2.45** (1.48–4.07)	**4.07** (1.94–7.85)	9	2
Spotfin shiner	*Cyprinella spiloptera*	3.07 (0 – >999)	3.07 (0.10–33.3)	7 (0.15–276)	3	1
Brassy minnow	*Hybognathus hankinsoni*	3.49 (0 – >999)	3.50 (0.67–17.5)	—	10	0
Brook trout	*Salvelinus fontinalis*	3.70 (0.36–62.7)	**3.70** (1.40–9.50)	0 (0–57)	12	1

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Table 1 *(concluded).*

Common name	Scientific name	CPUE ratio	OR	OR_c	Occurrence: One stream of a pair	Occurrence: Both streams of pair
Blacknose shiner	*Notropis heterolepis*	5.24 (0.61–70.5)	5.25 (0.91–27.9)	1.7 (0.25–23.9)	7	3
Bluegill	*Lepomis macrochirus*	6.00 (0.05–881)	6.00 (0.81–40.4)	—	5	0
Black bullhead	*Ameiurus melas*	188 (0.01 – >999)	**189** (24.8 – >999)	—	6	0
Black crappie	*Pomoxis nigromaculatus*	667 (0.47 – >999)	>999 (0.05 – >999)	—	3	0
Brown bullhead	*Ameiurus nebulosus*	>999 (0.61 – >999)	>999 (0.20 – >999)	—	4	0
Blackchin shiner	*Notropis heterodon*	>999 (0.56–12.1)	**>999** (10.5 – >999)	—	4	0
Greater redhorse	*Moxostoma valenciennesi*	**>999** (1.19 – >999)	>999 (0.5 – >999)	—	2	0

Note: Lower and upper 95% confidence limits are provided in parentheses for each measure. A value of 1 indicates the distribution of a species above and below real barriers on barrier streams is the same as the distribution of that species above and below hypothetical barrier locations on reference streams. Bold values have 95% confidence limits that do not include 1. Occurrence summarizes the number of stream pairs when a species was collected in at least one stream of a pair and when it was collected in both streams of a pair.

[a]The American Fisheries Society Publication No. 29 (*Common and Scientific Names of Fishes from the United States, Canada, and Mexico, 6th ed.*) lists both an eastern and a western blacknose dace. However, we identified the fish prior to this splitting of the species and treated our samples as one species.

covariance matrix for the transformed morphological measures was used to generate multivariate measures of size (PC1) and shape (PCs 2–4). Following the higher nodes approach of Harvey and Pagel (1991), analyses at the genus level used means of univariate or multivariate scores calculated from the species within each genus. Analyses at the family level used means of univariate or multivariate scores calculated from the genera within each family.

Results

Assessment of sensitive species

Eighty-one species from 49 genera and 16 taxonomic families were collected during our field survey. Of these, 48 species from 34 genera and 12 taxonomic families were abundant enough for us to calculate the measures of sensitivity (Tables 1–3).

Four key results were obtained from these analyses. First, 8–19 of the 48 most common species, 5–16 of 34 genera, and 2–7 of 12 taxonomic families showed signs of being sensitive to sea lamprey barriers based on the their longitudinal distributions within barrier and reference streams. Variation in the number of sensitive taxa is due to differences in the information considered and assumptions made by the three methods used to assess sensitivity. Depending on the measure considered, 6–12 species, 4–11 genera, and 1–5 families were underrepresented above barriers, while 2–7 species, 1–5 genera, and 1–2 families were overrepresented above barriers (Tables 1–3).

Second, the three measures of sensitivity were correlated reasonably strongly with each other at each taxonomic level considered (Table 4). At every level, correlations were highest between the unstratified OR and the CPUE ratio. These two measures were almost identical even though the OR did not consider variation in electroshocking time (Table 1); however, confidence intervals estimated for the CPUE ratio were wider than those for the OR. The weakest correlations were observed between the OR_c obtained after stratifying by stream pair and the other two measures (Table 4).

Third, there were instances where estimates of a taxon's sensitivity varied considerably between the OR_c and the other two measures, but these were relatively few. Examples included common carp (*Cyprinus carpio*), American brook lamprey (*Lampetra appendix*), smallmouth bass (*Micropterus dolomieu*), pumpkinseed (*Lepomis gibbosus*), brook trout (*Salvelinus fontinalis*), and the central mudminnow (*Umbra limi*). The first five examples are species that were not often found in both streams of a stream pair. Conversely, the central mudminnow was found in both streams of a pair in 12 of 19 instances (Table 1). In its case, the difference was due to two stream pairs that were not suitable for the OR_c calculation because mudminnows were only detected in stream sections above the barrier locations (see Materials and methods) and where the numbers of individuals detected above the hypothetical barrier locations were unusually high relative to other stream pairs.

Fourth, patterns observed at one taxonomic level were not necessarily reflected at another. With the family Percidae, for example, fishes from the genera *Perca* and *Percina* tended to be underrepresented above barriers, while fishes from the genus *Etheostoma* tended to be overrepresented (Table 2).

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Yet for percids overall, 95% confidence limits for the measures of sensitivity all included the value of 1 (Table 3), the value expected if the longitudinal distribution of percids observed for barrier streams was the same as that observed for reference streams. Similarly, some cyprinid species were relatively less abundant above barriers (e.g., longnose dace, *Rhinichthys cataractae*), but others were relatively more abundant above barriers (e.g., hornyhead chub, *Nocomis biguttatus*). However, the overall abundance of cyprinids above barrier locations relative to below tended to be lower for streams with lamprey barriers than for streams without lamprey barriers. Conversely, the two common species of the family Catostomidae, white sucker (*Catostomus commersonii*) and northern hog sucker (*Hypentelium nigricans*), tended to be less abundant above lamprey barriers than expected based on reference streams, but only the value of the OR_c for white sucker had confidence limits that did not include the value of 1 (Table 1). At the family level, however, the two OR measures of sensitivity indicated that abundances of catostomid fishes above sea lamprey barriers relative to below were consistently lower than expected based on reference streams (Table 3).

Taxonomic affiliation and sensitivity

Sensitivity to barriers was largely species specific. Taxonomic family accounted for 0%, 4%, and 2% of the total variance in the transformed values of the OR_c, OR, and CPUE ratio, respectively, (intraclass correlations = 0.00, 0.04, and 0.02, respectively). Genus within family accounted for 0%, 12%, and 39% of the total variance, respectively.

Morphology and sensitivity

We found no strong predictive relationships between our measures of sensitivity and any of the proposed morphological correlates of swimming performance and habitat use. The measures of sensitivity were not significantly correlated with univariate or multivariate measures of body size at any of the taxonomic levels considered (Table 5). The measures of sensitivity were also not significantly correlated with univariate and multivariate measures of body shape (Table 6). A summary of the principal components analysis of morphology is provided in Table 7.

Discussion

Assessment of sensitive species

The first noteworthy contribution of our study is the introduction of a rigorous, quantitative method for assessing the sensitivity of stream fishes to small, instream barriers and the application of this method to identify common fish taxa that appear to be sensitive to sea lamprey barriers, as judged by their longitudinal distribution in barrier streams relative to reference streams. Knowledge of sensitivity is needed to implement GLFC's Interim Policy on the Placement of Sea Lamprey Barriers, which was developed in response to our earlier findings that barriers alter species richness within streams (Dodd et al. 2003; Hayes et al. 2003) and restrict the movements of common fishes (Porto et al. 1999). Policy guidelines specify that construction of a barrier will not be recommended if the barrier is anticipated to negatively affect fish species at risk, reduce the diversity of fishes within the stream, lead to the loss of a fish species within the fish faunal region where the stream is found, or lead to a range reduction for species with fragmented distributions within the fish faunal region. Knowledge of sensitivity is also needed to prioritize species for fish passage research, given that over 100 fish species have been observed in the streams and rivers where sea lamprey spawn (R. McLaughlin, unpublished data).

At each of the taxonomic levels considered, the majority of taxa examined did not exhibit evidence of being sensitive to low-head barriers; however, a potentially meaningful proportion did. For many species, the differences in longitudinal distributions between barrier and reference streams were in degree, with individuals being detected above the barrier but with slightly lower odds of occurrence relative to their occurrence in reference streams (e.g., mottled sculpin, *Cottus bairdii*). However, for some species, such as yellow perch (*Perca flavescens*), no individuals were detected above sea lamprey barriers, but individuals were expected there based on their presence above hypothetical barrier locations on reference streams. The only sensitive species with conservation designations assigned by provincial or state management agencies were the blacknose shiner (*Notropis heterolepis*, endangered in Illinois) and the blackchin shiner (*Notropis heterodon*, threatened in Illinois and endangered in Ohio), which tended to be overrepresented above barriers. In addition, other sensitive species have been assigned Natural History Information Centre Rankings of very rare or rare to uncommon in certain political jurisdictions within the basin. Ultimately, whether the differences observed between species' distributions on barrier and references streams are considered acceptable depends on a complex decision weighing the benefits that sea lamprey control provides in the basin against the nontarget effects that control actions have in streams where they are carried out.

Predicting sensitivity from taxonomic affiliation and morphology

A second noteworthy contribution from our study is the finding that sensitivity to barriers is variable among closely related species, a result consistent with the emerging, general observation that species' responses to habitat fragmentation are often diverse and challenging to predict (Debinski and Holt 2000; Young and Clarke 2000). On the one hand, the species-specific responses are encouraging. Concerns regarding coincident losses or severe population declines for closely related species are not evident for sea lamprey barriers, although net changes in numbers were observed for some genera and families. The heterogeneity in responses also raises the possibility that certain species may be replaced by a related species of similar ecology, such that the ecosystem services provided by the assemblage are not altered even though the assemblage composition may change. This remains to be tested, however. On the other hand, the species specificity is disappointing because the sensitivity measured for one species does not appear to predict the sensitivity of a closely related species whose sensitivity is unknown.

A third noteworthy contribution from our study is the demonstration that the morphological correlates of general swimming performance and habitat use that were measured

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Table 2. Identification of genera sensitive to low-head barriers based on the catch-per-unit-effort (CPUE) ratio, odds ratio (OR), and common odds ratio (OR_c).

Genus	CPUE ratio	OR	OR_c	Occurrence	
				One stream of a pair	Both streams of a pair
Phoxinus	**0** (0–0.16)	**0** (0–0.11)	**0** (0–0.46)	12	2
Petromyzon	**0** (0–0.26)	**0** (0–0.48)	**0** (0–0.69)	11	3
Perca	0 (0–1.20)	**0** (0–0.68)	**0** (0–0.53)	9	2
Percopsis	0 (0–4.96)	0 (0–8.06)	0 (0–29.0)	4	1
Esox	**0.05** (0–0.45)	**0.05** (0.01–0.41)	0 (0–4.99)	9	1
Margariscus	0.14 (0–11.6)	0.14 (0.01–1.31)	—	6	0
Hypentelium	0.19 (0–423)	0.19 (0.01–2.60)	0.67 (0.01–11.6)	3	2
Exoglossum	**0.24** (0.07–0.74)	**0.24** (0.07–0.82)	**0.24** (0.07–0.82)	1	1
Umbra	0.27 (0.05–1.18)	**0.27** (0.17–0.43)	1.45 (0.76–3.20)	19	12
Pimephales	0.32 (0.16–1.62)	**0.32** (0.15–0.72)	0.45 (0.09–1.79)	16	4
Cyprinus	0.39 (0.01–20.4)	0.39 (0.09–1.73)	1.8 (0.15–94.19)	5	2
Percina	0.43 (0.13–1.34)	**0.43** (0.24–0.76)	**0.09** (0.02–0.27)	18	8
Culaea	0.47 (0.06–2.48)	0.47 (0.21–1.02)	**0.28** (0.07–0.92)	17	4
Micropterus	0.54 (0.08–4.21)	0.54 (0.15–2.02)	2.2 (0.39–11.8)	9	2
Lampetra	0.69 (0.03–12.7)	0.69 (0.23–2.13)	**10.5** (1.09–254)	6	1
Rhinichthys	0.69 (0.36–1.34)	**0.69** (0.61–0.78)	**0.86** (0.74–0.96)	24	23
Ambloplites	0.70 (0.29–1.72)	0.70 (0.45–1.11)	**0.36** (0.16–0.59)	22	10
Catostomus	0.83 (0.36–1.92)	0.83 (0.56–1.22)	**0.60** (0.35–0.99)	22	16
Luxilus	0.85 (0.28–2.52)	0.85 (0.59–1.20)	**0.45** (0.24–0.72)	17	10
Cottus	0.90 (0.41–1.99)	0.90 (0.76–1.07)	0.91 (0.72–1.11)	21	17
Noturus	1.10 (0.01–210)	1.10 (0.10–11.9)	—	4	0
Semotilus	1.11 (0.49–2.53)	1.11 (0.88–1.40)	**1.45** (1.16–2.14)	23	18
Oncorhynchus	1.21 (0.47–3.19)	1.21 (0.98–1.50)	**1.37** (1.02–2.04)	21	16
Etheostoma	1.25 (0.58–2.74)	**1.25** (1.02–1.54)	**1.81** (1.49–2.56)	22	15
Lepomis	1.53 (0.16–23.4)	1.53 (0.60–3.90)	**0.02** (0–0.77)	16	5
Salmo	1.71 (0.02–423)	1.71 (0.66–4.41)	1.8 (0.29–15.3)	13	2
Nocomis	2.39 (0.54–11.9)	**2.39** (1.44–3.93)	**4.07** (1.94–7.85)	9	2
Notropis	2.88 (0.46–19.69)	**2.89** (1.47–5.51)	3.09 (0.97–29.7)	15	3
Salvelinus	2.96 (0.33–34.1)	**2.96** (1.21–7.21)	0 (0–5.97)	12	2
Cyprinella	3.14 (0–444)	3.13 (0.10–33.9)	7 (0.15–276)	4	1
Hybognathus	3.49 (0.24–72.9)	3.5 (0.67–17.5)	—	9	0
Moxostoma	101 (0.05 – >999)	>999 (0.027 – >999)	—	6	0
Ameiurus	**354** (3.02 – >999)	**356** (49.0 – >999)	>999 (0.26 – >999)	10	1
Pomoxis	667 (0.47 – >999)	>999 (0.05 – >999)	—	3	0

Note: Lower and upper 95% confidence limits are provided in parentheses for each measure. A value of 1 indicates the relative abundances of fish from a given genera collected above versus below a barrier on barrier streams is the same as that observed above and below a hypothetical barrier on reference streams. Bold values have 95% confidence limits that do not include 1. Occurrence summarizes the number of stream pairs when a genus was collected in at least one stream of a pair and when it was collected in both streams of a pair.

here do not predict sensitivity to sea lamprey barriers. This finding is important because it suggests that sea lamprey barriers do not differentially affect fishes of certain body form. It is also important because we have encountered strong preconceptions that body size and shape should predict sensitivity and because our study explicitly tests the relationship at a geographic scale and taxonomic breadth that is unparalleled by earlier studies. The strong preconception is presumably a consequence of successes from the literature on functional and ecological morphology (Scarnecchia 1988; Wainwright and Reilly 1994; Matthews 1998).

The absence of a predictive relationship warrants greater consideration of the assumptions that underlie the expectation. One assumption is that our measures of sensitivity are a direct consequence of barriers restricting the normal movements of a given species. However, populations or subpopulations do not necessarily have to exhibit a decline following fragmentation. Indirect population responses are also possible. Some species were relatively more abundant than expected above sea lamprey barriers, which may reflect some form of ecological release in response to a predator or competitor being denied access to the stream segment above a barrier. A second assumption is that passage over or around a barrier is determined by swimming ability. This assumption fails to consider the importance of the sensory biology associated with finding a way past the barrier or other behavioural abilities that allow fishes to exploit heterogeneities in flow (Liao et al. 2003). Sea lampreys, for example, are considered to have poor swimming capacity, yet they successfully pass hydrodynamic challenges by using their oral

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Table 3. Identification of families sensitive to low-head barriers based on the catch-per-unit-effort (CPUE) ratio, odds ratio (OR), and common odds ratio (OR_c).

Family	CPUE ratio	OR	OR_c	Occurrence	
				One stream of a pair	Both streams of a pair
Percopsidae	0.00 (0.00–4.96)	0 (0–8.06)	0 (0–29.0)	4	1
Esocidae	**0.05** (0.00–0.45)	**0.05** (0.01–0.41)	0 (0–4.99)	9	1
Gasterosteidae	0.27 (0.05–1.17)	**0.27** (0.14–0.54)	**0.21** (0.02–0.17)	15	6
Umbridae	0.27 (0.05–1.18)	**0.27** (0.17–0.43)	1.45 (0.76–3.20)	19	12
Catostomidae	0.57 (0.23–1.32)	**0.56** (0.40–0.79)	**0.51** (0.30–0.80)	23	18
Cyprinidae	0.79 (0.44–1.42)	**0.79** (0.72–0.87)	**0.87** (0.77–0.95)	24	24
Petromyzontidae	0.87 (0.13–5.75)	0.88 (0.36–2.12)	1.33 (0.40–5.40)	15	5
Cottidae	0.90 (0.41–1.99)	0.90 (0.76–1.07)	0.91 (0.71–1.11)	21	17
Centrarchidae	0.94 (0.39–2.32)	0.94 (0.65–1.34)	1.07 (0.71–1.71)	23	11
Percidae	0.94 (0.48–1.82)	0.94 (0.78–1.13)	1.16 (0.95–1.49)	24	19
Salmonidae	1.66 (0.66–4.40)	**1.66** (1.38–2.00)	**1.55** (1.22–2.26)	23	17
Ictaluridae	**77.7** (4.44 – >999)	**78.0** (22.6–260)	**170** (22.7–1029)	10	2

Note: Lower and upper 95% confidence limits are provided in brackets for each measure. A value of 1 indicates the relative abundances of fish from a given taxonomic family collected above versus below a barrier on barrier streams is the same as that observed above and below a hypothetical barrier on reference streams. Bold values have 95% confidence limits that do not include 1. Occurrence summarizes the number of stream pairs when a taxonomic family was collected in at least one stream of a pair and when it was collected in both streams of a pair.

disc to attach periodically to surfaces. A third assumption is that swimming ability is influenced by body size and shape. There is a rich literature demonstrating that broad correlations exist (Webb 1984, 1988; Matthews 1998). Still, the functional relationships among behaviour, performance, and morphology are often complex and poorly examined (Lauder 1996; Matthews 1998), and the broad correlations may be difficult to observe and detect over a narrower range of body sizes and shapes (Smith 1980). Most of the species in our study were of similar body form and have been described as locomotor generalists (Webb 1984).

Table 4. Kendall's rank correlation coefficients comparing the catch-per-unit-effort (CPUE) ratio, odds ratio (OR), and common odds ratio (OR_c).

	Species		Genus		Family	
	OR (48)	OR_c (35)	OR (34)	OR_c (28)	OR (12)	OR_c (12)
CPUE ratio	0.98	0.55	0.99	0.50	0.97	0.72
OR	—	0.56	—	0.49	—	0.69

Note: Number of taxa are shown in parentheses.

Strengths and weaknesses of our method of assessing sensitivity

The measures used to assess sensitivity to sea lamprey barriers have four attractive features. The first of these features is statistical sensitivity. We were able to identify sensitive taxa at each taxonomic level even though sample sizes were low for some species (e.g., northern pike, *Esox lucius*). A second feature is interpretability. This feature is enhanced through the inclusion of comparative data for reference streams and, for species with broader distributions, the consideration of multiple stream pairs. Without references, it is challenging, if not impossible, to distinguish any effect of a dam from natural variation or from other potential sources of effect (Hayes et al. 2003). Efforts to assess the effects of small dams have often lacked reference locations (Peter 1998; Helfrich et al. 1999). Consideration of multiple stream pairs allows us to focus on the general effects of sea lamprey barriers rather than on the effects of any specific dam (Hayes et al. 2003). A third feature of our analysis is coherence. Estimates of sensitivity from the three methods employed here were correlated reasonably highly despite variation in the data used by each method. A final feature is transparency. The information and criteria used to assess sensitivity in this study are clearer than those typically used in past assessments of sensitivity or in assignments of conservation designations (Jones and Kaly 1996; Musick 1999).

There are also six limitations and uncertainties with our measures of sensitivity. First, our analyses were restricted to the most common species collected in our extensive field survey because of limitations on sample size, yet the rarer species may be of greatest conservation concern. Our field survey also did not detect all of the stream fishes that co-occur with sea lampreys. This creates the need to either spend more time and money assessing the remaining species or to seek effective predictors of sensitivity (Dulvy and Reynolds 2002; Reed and Shine 2002). Second, estimates of sensitivity for some species differed substantially from a value of 1, presenting possible reason for concern, yet had wide confidence limits that included the value of 1. The point estimates of 0 for trout-perch (*Percopsis omiscomaycus*) provide such examples. Trout-perch is known to migrate between the lakes and tributaries, but is not noted for being a strong swimmer (Scott and Crossman 1973), which suggests movements of this species could be blocked by instream barriers. Improving estimates through more intensive sampling at a site (e.g., triple pass electrofishing, addition of blocking nets) would have been desirable, but was not practical given the time constraints on our fieldwork. Further, increasing precision at a single site is not necessarily more informative than sampling more sites less precisely, unless it is known that replicate sites exhibit similar responses to the perturbation (Walters and Green 1997). Third, our survey did not include data collected prior to barrier construction. Designs

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Table 5. Kendall's rank correlation coefficients relating univariate and multivariate measures of body size (principal component 1; PC 1) for stream fish taxa to two measures of their sensitivity to low-head barriers: the catch-per-unit-effort (CPUE) ratio and common odds ratio (OR_c).

	Species		Genus		Family	
Measure of size	CPUE ratio	OR_c	CPUE ratio	OR_c	CPUE ratio	OR_c
Univariate						
Fork length (this study)	0.07	–0.05	0.09	0.06	0.15	0.05
Total length (Trautman 1981)	0.02	–0.16	0.04	–0.14	0.13	–0.07
Multivariate						
PC 1 (Trautman 1981)	0.04	–0.16	0.15	–0.05	0.10	0.11

Table 6. Kendall's rank correlation coefficients relating multivariate measures of body shape (principal components 2 and 3; PCs 2 and 3) for stream fish taxa to two measures of their sensitivity to low-head barriers: the catch-per-unit-effort (CPUE) ratio and common odds ratio (OR_c).

	Species		Genus		Family	
Measure of shape	CPUE ratio (39)	OR_c (29)	CPUE ratio (27)	OR_c (23)	CPUE ratio (11)	OR_c (11)
PC 2	–0.21	0.04	–0.31	–0.05	–0.10	–0.22
PC 3	–0.09	–0.02	–0.05	–0.13	–0.28	–0.29

Note: Number of taxa are shown in parentheses.

Table 7. Eigenvectors from a principal components (PC) analysis summarizing variation in six morphological features expected to influence the swimming ability and use of fast-flowing water for 69 stream fishes.

	Eigenvectors			
Morphological feature	PC 1	PC 2	PC 3	PC 4
Total length	0.41	–0.04	0.52	–0.02
Body depth	0.46	–0.23	–0.56	–0.28
Minimum caudal peduncle depth	0.43	–0.12	–0.29	0.79
Caudal peduncle length	0.28	0.95	–0.06	0.02
Maximum caudal fin depth	0.45	–0.01	–0.08	–0.54
Caudal fin length	0.40	–0.16	0.57	0.08
% of variance	94	4	1	<1

including before and after data for barrier and reference streams would be most desirable for detecting the effects of a barrier against a background of natural and other anthropogenic changes (Hayes et al. 2003); however, adequate historical records were not available for our study streams (Ross 2001), and considerable time will be needed before they are available for streams scheduled for barrier construction. Fourth, our estimates of sensitivity are limited to a single field season. Longitudinal distributions of fishes may vary seasonally and annually because of migratory movements within the stream sections above and below barriers and, possibly, because of movement between sections if a barrier becomes inundated. Fifth, our study design is not suitable for detecting species that have disappeared from the entire stream following construction of a barrier. Lastly, our analyses identify species that appear to be sensitive to barriers, but do not identify specific mechanisms for each species' sensitivity. We have deliberately restricted ourselves to the former because of the uncertainty regarding if and how species traverse the barriers, the diversity of mechanisms that might influence longitudinal abundances following stream fragmentation, and the inadequacy of our data for examining these mechanisms directly.

Which measure of sensitivity warrants the strongest consideration is unclear. Values for the CPUE ratio and OR were almost identical and therefore provide a similar estimate of sensitivity. Relative to both of the OR measures, the CPUE ratio has the advantage of incorporating sampling effort. This did not matter much in our study, because the allocation of effort above and below barrier locations was similar for barrier and reference streams, but it could be important in other study designs. The CPUE ratio has the disadvantage of having wider confidence limits than the ORs. Unlike the other measures, the OR_c, which stratifies across stream pairs, helps avoid the loss information arising when data are aggregated (Simpson's paradox) (Mittal 1991; Moore and McCabe 1999); however, in our case it only uses that subset of information available from stream pairs where a species is found in both streams of a pair and at least one of the stream sections above a barrier location and at least one

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below. For some species in our study, this limited the number of stream pairs and individuals used in the calculation (e.g., American brook lamprey and brook trout).

In conclusion, our study introduces and applies an explicit and rigorous means of evaluating the sensitivity of fishes to small, instream barriers and identifies sources of uncertainty with these evaluations. It also represents the first large-scale, comprehensive effort to assess the sensitivity of stream fishes to instream barriers. Although further validation is needed, our estimates of sensitivity will help natural resource and aquatic managers in the Great Lakes to anticipate how common stream fishes could respond to the construction or removal of instream barriers, as well as to assist scientists with the prioritization of species for passage research. In addition, the estimates may prove useful in other geographic areas because many of the fishes have distributions extending outside of the basin. Predicting or measuring sensitivity to barriers for the other stream fishes known to co-occur with sea lampreys in the Great Lakes remains an important outstanding challenge.

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Appendix A

Table A1. Species summaries of the numbers of individuals caught above and below real barriers on barrier streams and hypothetical barrier locations on reference streams.

	Stream type			
	Barrier		Reference	
Scientific name	Above (*a*)	Below (*b*)	Above (*c*)	Below (*d*)
Ambloplites rupestris	87	170	53	73
Ameiurus melas	6	3	2	189
Ameiurus natalis	1	0	0	0
Ameiurus nebulosus	8	1	0	1
Amia calva	0	2	0	1
Anguilla rostrata	0	1	0	0
Campostoma anomalum	0	12	0	0
Catostomus commersoni	107	168	83	108
Cottus bairdii	480	596	448	446
Cottus cognatus	72	12	0	0
Couesius plumbeus	19	135	0	0
Culaea inconstans	84	45	40	10
Cyprinella lutrensis	1	0	0	0
Cyprinella spiloptera	46	3	5	1

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Table A1 (*continued*).

Scientific name	Stream type			
	Barrier		Reference	
	Above (*a*)	Below (*b*)	Above (*c*)	Below (*d*)
Cyprinus carpio	9	23	5	5
Esox lucius	4	8	19	2
Etheostoma caeruleum	22	27	157	192
Etheostoma exile	0	12	1	2
Etheostoma flabellare	108	45	132	102
Etheostoma nigrum	192	204	170	220
Exoglossum maxillingua	25	47	11	5
Gasterosteus aculeatus	0	65	0	2
Gymnocephalus cernuus	0	2	0	0
Hybognathus hankinsoni	14	4	6	6
Hypentelium nigricans	1	2	70	27
Ichthyomyzon castaneus	1	0	0	0
Ichthyomyzon fossor	16	4	0	0
Ictalurus punctatus	0	1	0	0
Lampetra appendix	67	73	8	6
Lepomis cyanellus	3	21	0	0
Lepomis gibbosus	8	69	5	53
Lepomis macrochirus	3	5	3	30
Lota lota	0	86	0	5
Luxilus chrysocephalus	0	1	3	0
Luxilus cornutus	225	198	108	83
Margariscus margarita	10	18	4	1
Micropterus dolomieu	6	27	2	8
Micropterus salmoides	1	12	3	7
Morone chrysops	0	1	0	1
Moxostoma anisurum	0	1	0	1
Moxostoma erythrurum	0	4	0	1
Moxostoma valenciennesi	1	0	0	1
Notemigonus crysoleucas	96	74	37	70
Notemigonus micropogon	0	0	1	0
Notemigonus crysoleucas	0	4	0	2
Notropis atherinoides	0	3	0	0
Notropis heterodon	5	3	0	45
Notropis heterolepis	18	8	3	7
Notropis photogenis	0	0	0	4
Notropis rubellus	6	30	21	61
Notropis volucellus	0	5	0	0
Noturus flavus	11	10	2	2
Oncorhynchus kisutch	6	3	66	24
Oncorhynchus mykiss	416	224	466	318
Oncorhynchus tshawytscha	0	0	1	5
Opsopoeodus emiliae	0	0	0	1
Perca flavescens	0	16	16	35
Percina caprodes	4	109	31	72
Percina maculata	24	39	4	8
Percina shumardi	0	2	0	0
Percopsis omiscomaycus	0	6	2	11
Petromyzon marinus	0	19	4	6
Phoxinus eos	29	45	30	0
Phoxinus erythrogaster	1	0	0	0
Phoxinus neogaeus	0	1	0	0
Pimephales notatus	22	57	5	18
Pimephales promelas	4	21	16	2
Pomoxis nigromaculatus	1	1	0	2
Pungitius pungitius	0	0	0	2

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Table A1 (*concluded*).

Scientific name	Stream type			
	Barrier		Reference	
	Above (*a*)	Below (*b*)	Above (*c*)	Below (*d*)
Pylodictis olivaris	0	1	0	0
Rhinichthys atratulus	637	539	588	489
Rhinichthys cataractae	312	795	568	635
Salmo salar	0	0	0	2
Salmo trutta	11	8	212	262
Salvelinus fontinalis	77	8	39	15
Salvelinus namaycush	0	2	0	0
Semotilus atromaculatus	294	316	234	283
Semotilus corporalis	2	3	4	1
Sander canadensis	0	3	0	1
Sander vitreus	0	1	0	0
Umbra limi	115	63	264	39

Note: *a*, *b*, *c*, and *d* correspond to the components of eq. 1.

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Underwater but not out of sight: genetic monitoring of effective population size in the endangered North Sea houting (*Coregonus oxyrhynchus*)

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Abstract: We analysed 12 microsatellite DNA loci in temporal samples (1980, 1994, and 2002) from the only remaining indigenous population of the North Sea houting (*Coregonus oxyrhynchus*) in the Vidaa River, Denmark. Using a novel temporal method, we estimated effective population size (N_e) to be 577.4 (90% highest posterior density limits 297.2–3719.8). The same method was used to estimate N_e at the beginning and end of the sampled time interval, and the results were indicative of a relatively stable population. In contrast, tests for recent bottlenecks suggested population declines in the 1980 and 1994 samples, possibly reflecting declines prior to 1980 in the total North Sea houting population. To evaluate the usefulness of the two methods for routine genetic monitoring, we simulated population declines corresponding to reproduction by only 20 or 50 parents in 2002. For both simulated samples, the temporal method provided evidence for a population decline, whereas the test for bottlenecks did not suggest population decline. We conclude that the North Sea houting in the Vidaa River is not immediately threatened by inbreeding or loss of evolutionary potential, and the applied temporal method appears very useful for genetic monitoring of effective population size in endangered, isolated fish populations.

Résumé : Nous avons analysé 12 locus microsatellites d'ADN dans des échantillons répartis dans le temps (1980, 1994 et 2002) provenant de la seule population indigène survivante du houting de la mer du Nord (*Coregonus oxyrhynchus*) dans la Vidaa, Danemark. À l'aide d'une méthode temporelle nouvelle, nous avons estimé la taille effective de la population (N_e) à 577,4 (limites à 90 % de la densité a posteriori la plus élevée, 297,2–3719,8). La même méthode a servi à estimer N_e au début et à la fin de l'intervalle d'échantillonnage et les résultats indiquent que la population est relativement stable. En revanche, des tests pour l'existence de goulots d'étranglement récents laissent croire à des déclins de population dans les échantillons de 1980 et de 1994, qui reflètent peut-être des déclins dans l'ensemble de la population de houtings de la mer du Nord avant les années 1980. Afin d'évaluer l'utilité des deux méthodes pour une surveillance génétique de routine, nous avons simulé des déclins de population correspondant à une reproduction par seulement 20 ou 50 parents en 2002. Dans les deux échantillons simulés, la méthode temporelle fournit des indices d'un déclin de population, alors que le test pour les goulots d'étranglement n'indique aucun déclin. Nous en concluons que le houting de la mer du Nord de la Vidaa n'est pas menacé dans l'immédiat par la consanguinité ou par la perte de potentiel évolutif et que la méthode temporelle utilisée semble très commode pour suivre la taille effective des populations de poissons isolées et menacées.

[Traduit par la Rédaction]

Introduction

Monitoring population sizes is an integral part of conservation and management programs. The rate of inbreeding and genetic drift is determined by the effective population size (N_e), which is defined as the number of individuals in an idealized population (i.e., with equal sex ratio and variance in family size approximated by a Poisson distribution) that would cause the same rate of inbreeding or genetic drift as that of the actual population in question (Frankham et al. 2002). In real populations, however, temporal fluctuations of N_e occur, and there may be unequal sex ratio and high variance in family size. As a result, the effective population size is nearly always considerable lower than the census population size (Frankham 1995). It has previously been argued that demographic and environmental stochasticity would lead to extinction risk at population sizes too high for inbreeding to be a problem, hence making genetic concerns of minor importance (Lande 1988). Recently, however, empirical results have demonstrated that inbreeding interacts with demo-

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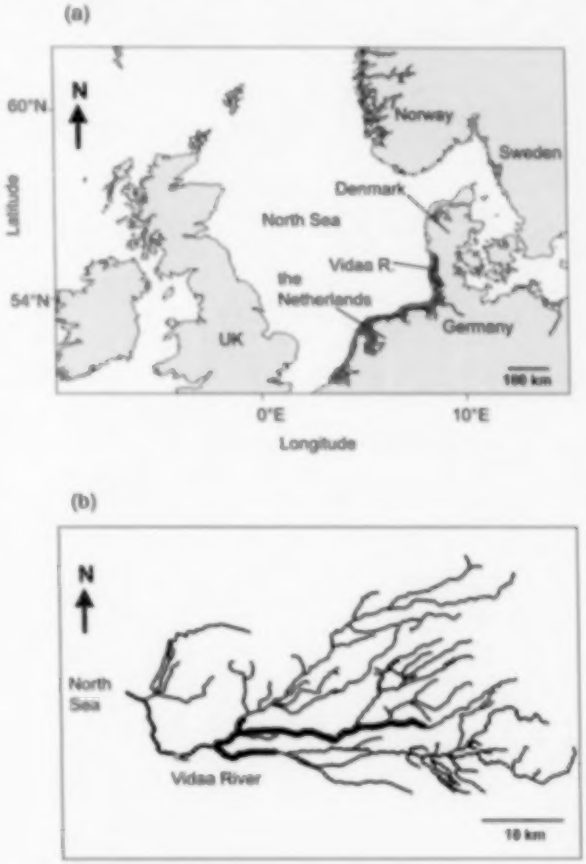
graphic and environmental factors to increase extinction risk in wild populations (Saccheri et al. 1998). Therefore, it is important to obtain knowledge on both census and effective population sizes in endangered populations.

N_e can be estimated using molecular markers (Waples 1991), and among these methods the temporal method (Waples 1989) appears to provide the most reliable results. The principle is to analyse molecular markers in two or more temporal samples from the population in question and then estimate the variance effective population size based on the temporal changes of allele frequencies that have occurred because of genetic drift. Furthermore, a number of other methods exist that do not specifically estimate N_e but provide tests for recent population declines (e.g., Cornuet and Luikart 1996; Garza and Williamson 2001). Methods for estimating N_e and population declines are applied increasingly in studies of fish populations, both for analysing the factors shaping the genetic structure of populations (e.g., Miller and Kapuscinski 1997; Hansen et al. 2002; Fraser et al. 2004) and for obtaining information on N_e in populations of conservation concern (e.g., Waples 1990; Hedrick et al. 2000; Saillant et al. 2004). However, there are still few examples of integration of N_e estimates in monitoring programs for endangered species and populations.

In this study, we focus on the North Sea houting (*Coregonus oxyrhynchus*), an anadromous coregonid fish that was previously distributed throughout the Wadden Sea area of the North Sea, including major rivers like the Rhine and Elbe. As is generally the case for coregonid fishes, the taxonomy to date is chaotic, and whether or not North Sea houting and common whitefish (*Coregonus lavaretus*) are good biological species according to a biological species concept (i.e., show reproductive isolation in sympatry) remains uncertain (Hansen et al. 1999). However, the North Sea houting exhibits special adaptations to oceanic salinities and would undoubtedly qualify as an evolutionarily significant unit (see discussion in Hansen et al. 1999). Nearly all populations of North Sea houting were extirpated during the twentieth century, owing primarily to river regulation and pollution. It is assumed that only one indigenous population remains, which is found in the Danish Vidaa River (see Fig. 1*a*). Electrofishing surveys suggest that the current spawning population totals ~4000 individuals (Jensen et al. 2003). The neighbouring rivers Ribe, Varde, and Sneum contain small and declining populations (Jensen et al. 2003), but results from a study employing microsatellite and mitochondrial DNA analysis suggest that at least two of the populations are remains of reintroduction efforts based on stocking with Vidaa River North Sea houting (Hansen et al. 1999). In the 1980s–1990s, supportive breeding and stocking was the preferred management option, but today attention has shifted towards habitat restoration and removal of migration barriers within rivers. The species has been protected in Denmark since 1983, it was included in the Berne Convention in 1988, and the Vidaa River and other rivers previously or presently inhabited by North Sea houting are now protected under the EU (European Union) Habitat Directive.

The purpose of this study was to obtain information on N_e and possible population declines in the North Sea houting population in the Vidaa River. We analysed variation at twelve microsatellite loci in three temporal samples from 1980, 1994, and 2003. We applied tests for recent population declines and estimated N_e using a novel method that provides estimates of N_e at the beginning and end of the time interval covered by temporal samples. This was done to answer the following questions: (*i*) What is the N_e of the Vidaa River North Sea houting population? (*ii*) Are there indications of population declines prior to and during the time interval covered by samples? (*iii*) Will genetic monitoring be useful for detecting possible future declines of N_e?

Fig. 1. (*a*) Map showing the location of the Vidaa River and the approximate historical distribution range of North Sea houting (*Coregonus oxyrhynchus*) in the Wadden Sea (North Sea) denoted by shaded areas. (*b*) Map showing the Vidaa River system. The spawning grounds of the North Sea houting are indicated by thick black lines.



Materials and methods

Microsatellite analysis

We analysed three temporal samples of spawning North Sea houting from the Vidaa River caught by electrofishing on the known spawning grounds of the population (see Fig. 1*b*) in December 1980 (N = 39), 1994 (N = 40), and 2002 (N = 50). The 1980 sample consisted of archived scales, whereas the 1994 and 2002 samples consisted of adipose fin tissue stored in 96% ethanol. DNA was extracted from scale sam-

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ples using the procedures described by Nielsen et al. (1999) and from tissue samples using the chelex–proteinase K protocol by Estoup et al. (1996). We analysed 12 microsatellite loci (annealing temperatures are given in parentheses): *Sfo23* (54 °C) (Angers et al. 1995), *Bwf1* (52 °C) and *Bwf2* (54 °C) (Patton et al. 1997), *BFRO018* (58 °C) (Susnik et al. 1999), *C2-157* (60 °C) (Turgeon et al. 1999), *Cocl-Lav1* (52 °C), *Cocl-Lav4* (56 °C), *Cocl-Lav6* (56 °C), *Cocl-Lav18* (58 °C), *Cocl-Lav27* (56 °C), *Cocl-Lav49* (56 °C), and *Cocl-Lav52* (62 °C) (Rogers et al. 2004). A further six loci (not listed) were discarded because of pronounced homozygote excesses in the 1980 sample, which the MICRO-CHECKER software (Van Oosterhout et al. 2004) suggested to be due to null alleles or large allele dropouts. The amplified loci were analysed on a Pharmacia ALFexpress automated sequencer according to recommendations by the manufacturer (Pharmacia AB, Stockholm, Sweden).

Statistical treatment

Deviations from Hardy–Weinberg equilibrium were tested by exact tests (Guo and Thompson 1992) using GENEPOP 3.1d (Raymond and Rousset 1995). Genetic variation within samples was quantified by observed (H_o) and expected (H_e) heterozygosity and by allelic richness (El Mousadik and Petit 1996), a measure of the number of alleles independent of sample size. Genetic differentiation between pairs of samples was tested by permuting genotypes between samples using a test by Goudet et al. (1996). The program FSTAT 2.9.1 (Goudet 1995) was used for these analyses.

We estimated N_e using the temporal method and TMVP software developed by Beaumont (2003). N_e is estimated based on two or more samples from the same population separated by a given number of generations. It is assumed in the model that the population is closed (i.e., there is no immigration). The method is based on coalescence theory, which provides a good approximation to a case with overlapping generations and uses Markov chain Monte Carlo (MCMC) simulations for generating a posterior distribution of N_e values. It incorporates Bayesian prior information by making the user specify a maximum N_e (N_{emax}), resulting in a uniform prior distribution of N_e from 0 to N_{emax}. Furthermore, the method allows for both estimating N_e over the entire time interval covered by samples and estimating N_e at the beginning and end of the sampled interval, incorporating a model of exponential change of N_e. The latter option provides information on whether or not N_e is declining, expanding, or stable, and this can further be tested by the "Bayes factor", which can be described as a Bayesian type of hypothesis testing. Bayes factors between 3 and 10 or between 1/3 and 1/10 are usually considered as moderate evidence in favour of one hypothesis over another, whereas Bayes factors >10 and <1/10 are considered as strong evidence. In the present case, where hypotheses of both population decline and expansion have the same prior probability, the Bayes factor is simply the proportion of MCMC iterations, where $N_A > N_0$ (decline) relative to the number of iterations, where $N_0 > N_A$ (expansion) (Beaumont 2003). Here, N_0 denotes effective population size over the most recent sampling interval, whereas N_A denotes effective population size at the oldest part of the time interval covered by samples. We based our analyses on 20 000 MCMC replicates and assumed N_{emax} values of 1000, 2000, and 4000 (based on the assumption that N_e is unlikely to be higher than the census population sizes of ~4000). Mean age of spawners was used as an approximation to generation length and was estimated to 4.0 years, based on scale readings of spawning Vidaa River North Sea houting (Hvidt and Christensen 1990).

We were interested in not only estimating N_e from 1980 to the present, but also in assessing the utility of Beaumont's (2003) method for detecting current time declines of N_e in North Sea houting. Therefore, we simulated population declines by randomly drawing 20 and 50 individuals from the 2002 sample. These samples were then arbitrarily split into two samples to represent two sexes (i.e., the 20 individuals were split into 10 males and 10 females, and the 50 individuals were split into 25 males and 25 females). We then simulated 50 offspring by randomly drawing alleles from the males and females, using the program HYBRIDLAB (Nielsen et al. 2001). In this model, all males and females contribute gametes to a common pool from which offspring are then generated by random fusion of gametes. Even though the model may be oversimplified compared with the mating system in real North Sea houting, we found it to be sufficient for the present purpose, as Beaumont's (2003) method is based on allele counts and does not take individual genotypes and correlation between alleles within individuals into account. We assumed that the simulated offspring were sampled one generation after the 2002 sample (i.e., in 2006), and we estimated N_e from 1980 to 2006 using the TMVP software (Beaumont 2003). All results of the TMVP analyses were reported as the modes and 90% highest posterior density (HPD) limits.

To compare the results obtained using TMVP with other previously published methods for estimating N_e, we also applied the pseudo-maximum likelihood temporal method by Wang (2001), using the software MLNE 2.3 (Wang and Whitlock 2003).

We also tested for recent bottlenecks using the method and software M_P_VAL by Garza and Williamson (2001). The method is based on estimating M, the ratio of the number of alleles to the range in allele size, which is expected to be reduced after a bottleneck. The significance of M was estimated by simulating the distribution of M values in a stable population with a θ value realistic for the populations analysed. Here, θ is defined as $4N_e\mu$, where N_e denotes the prebottleneck effective population size and μ is the mutation rate. We assumed θ values of either 1.0 or 4.0 (e.g., corresponding to N_e of 250 or 1000 and μ of 10^{-3}, or N_e of 2500 or 10 000 and μ of 10^{-4}, respectively). Finally, as recommended by Garza and Williamson (2001), we assumed a two-phase model of mutation (di Rienzo et al. 1994), where 90% of all mutations involved single step mutations and 10% involved on average 3.5 repeat units. We conducted the analyses both for the samples from 1980, 1994, and 2002 and for the simulated samples representing population declines.

Results

The total number of alleles ranged from 3 at the loci *Cocl-Lav18* and *Cocl-Lav27* to 16 at the locus *Sfo23* (Table 1). There were no trends towards a decrease of allelic richness

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Table 1. Summary of statistics for the studied microsatellite loci.

	Year of sampling		
	1980	1994	2002
***Sfo23* (total = 16; range = 161–195 bp)**			
AR	10.85	11.77	11.63
H-W test	0.143	0.029	0.071
H_o	0.846	0.925	0.840
H_e	0.849	0.824	0.823
N	39	40	50
***BWF1* (total = 8; range = 211–229 bp)**			
AR	8.00	6.99	7.00
H-W test	0.175	0.936	0.491
H_o	0.718	0.675	0.760
H_e	0.781	0.705	0.750
N	39	40	50
***BWF2* (total = 6; range = 150–162 bp)**			
AR	6.00	6.00	5.74
H-W test	0.339	0.548	0.212
H_o	0.763	0.775	0.700
H_e	0.746	0.785	0.734
N	39	40	50
***BFRO018* (total = 5; range = 188–198 bp)**			
AR	4.95	4.00	4.92
H-W test	0.851	0.297	0.327
H_o	0.692	0.625	0.640
H_e	0.654	0.620	0.640
N	39	40	50
***Cocl-Lav1* (total = 4; range = 239–251 bp)**			
AR	3.95	4.00	3.00
H-W test	0.492	0.000	0.159
H_o	0.462	0.400	0.660
H_e	0.547	0.572	0.583
N	39	40	50
***Cocl-Lav4* (total = 5; range = 146–154 bp)**			
AR	3.97	3	4.41
H-W test	0.17	1	1
H_o	0.211	0.2	0.3
H_e	0.22	0.187	0.267
N	38	40	50
***Cocl-Lav6* (total = 8; range = 121–149 bp)**			
AR	7.95	6	7.66
H-W test	0.854	0.113	0.034
H_o	0.846	0.825	0.6
H_e	0.76	0.737	0.693
N	39	40	50
***Cocl-Lav18* (total = 3; range = 150–158 bp)**			
AR	3	3	3
H-W test	0.829	0.159	0.436
H_o	0.59	0.475	0.5
H_e	0.512	0.497	0.458
N	39	40	50

Table 1 (*concluded*).

	Year of sampling		
	1980	1994	2002
***Cocl-Lav27* (total = 3; range = 183–187 bp)**			
AR	2.95	2	2.93
H-W test	1	0.396	0.444
H_o	0.205	0.175	0.28
H_e	0.189	0.202	0.331
N	39	40	50
***Cocl-Lav49* (total = 9; range = 167–187 bp)**			
AR	8	8.93	7.74
H-W test	0.976	0.642	0.984
H_o	0.892	0.85	0.9
H_e	0.865	0.853	0.831
N	37	40	50
***Cocl-Lav52* (total = 15; range = 115–161 bp)**			
AR	14.89	10	10.69
H-W test	0.316	0.274	0.962
H_o	0.974	1	0.98
H_e	0.897	0.866	0.878
N	39	40	50
***C2-157* (total = 8; range = 122–172 bp)**			
AR	6	7.9	6.85
H-W test	0.283	0.034	0.511
H_o	0.605	0.564	0.74
H_e	0.775	0.729	0.742
N	38	39	50

Note: Total, total number of observed alleles per locus; allele size ranges for the loci are also shown in parentheses; AR, allelic richness based on the smallest sample size in the data set (i.e., $N = 37$ for locus *Cocl-Lav49* in 1980); H-W test, outcome of tests for deviations from expected Hardy–Weinberg proportions; H_e, expected heterozygosity; H_o, observed heterozygosity; N, sample sizes of the studied populations.

or expected heterozygosity from 1980 to 2002. Thirty-six tests for Hardy–Weinberg equilibrium resulted in four outcomes with $p < 0.05$ (Table 1). However, only one test remained significant at the 5% level after sequential Bonferroni correction (initial $k = 12$). Pairwise tests for genetic differentiation (Goudet et al. 1996) resulted in no significant outcomes (data not shown).

For estimating N_e using TMVP (Beaumont 2003), we assumed three different N_{emax} values (i.e., 1000, 2000, and 4000). Inspection of the posterior density distributions showed that N_{emax} of 1000 was insufficient to obtain a reliable posterior distribution, whereas the modes and lower 90% HPD limits were consistent for N_{emax} values of 2000 and 4000, though the upper HPD limits increased with increasing N_{emax}. Since N_{emax} of 4000 corresponds to the census population size estimate, we chose to report the results based on this value. The point estimate of N_e over the entire time interval from 1980 to 2002 was 577.4 (90% HPD limits: 297.2–3719.8) (Table 2). Thus, N_e is unlikely to be lower than ~300, and we cannot rule out that N_e is much higher (though unlikely to be higher than the assumed spawning census population size of 4000).

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Table 2. Estimates of effective population size (N_e) using the temporal method by Beaumont (2003) and assuming an upper limit of N_e of 4000.

	Empirical data			Simulated decline			
				20 parents		50 parents	
	N_e: 1980–2003	N_A: 1980	N_0: 2002	N_A: 1980	N_0: 2006	N_A: 1980	N_0: 2006
Mode	577.4	457.3	489.4	701.5	38.8	417.3	69.8
90% HPD limits	297.2–3719.8	213.2–3823.9	249.2–3883.9	353.3–3759.8	25.4–134.2	165.1–3507.6	39.8–393.3
Bayes factor	—	0.865		152.846		11.121	

Note: N_e was estimated for the entire sampled time interval and for the beginning (N_A) and end (N_0) of the time interval. In the latter case, the statistical support for the hypothesis of population decline vs. population expansion was assessed by the Bayes factor (the proportion of Markov chain Monte Carlo iterations, where $N_A > N_0$ (decline) relative to the number of iterations, where $N_0 > N_A$ (expansion)). The analyses were conducted both for the empirical temporal samples (1980–2002) and for simulated population declines (1980–2002 and simulated samples from 2006). HPD, highest posterior density limits.

The point estimates of effective population size at the beginning (1980; N_A) and end (2002; N_0) of the sampled time interval were similar (457.3 and 489.4, respectively), but at the same time with wide HPD limits (Table 2). The Bayes factor was 0.865, thus providing no evidence for either population decline or expansion. We interpret this result as indicative of a relatively stable population. In contrast, analysis of temporal samples including the simulated population declines yielded strong evidence for declining N_e, with a Bayes factor of 152.846 for the simulated decline involving 20 parents and a Bayes factor of 11.121 for the decline involving 50 parents (Table 2). Even though the simulated declines could be detected with considerable statistical confidence, there was also a tendency towards higher estimates of N_0 as compared with the simulated numbers of parents (Table 2).

Estimation of N_e from 1980 to 2002 using the pseudo-maximum likelihood method by Wang (2001) and assuming N_{emax} of 4000 yielded a point estimate of 522.3 (95% confidence interval: 213.7 – >4000). This result must be considered congruent with the estimate obtained using TMVP (Table 2). An additional analysis assuming N_{emax} of 10 000 still resulted in an undefined upper confidence limit.

Analysis of recent population declines using the method by Garza and Williamson (2001) yielded significant outcomes for all samples assuming $\theta = 1.0$ and in two of the samples assuming $\theta = 4.0$ (Table 3). However, close inspection of the loci revealed outlier alleles (i.e., rare alleles separated by many repeat units) at the loci *C2-157* (outlier alleles separated by 11 repeat units) and *Cocl-Lav52* (outlier alleles separated by 5 repeat units), contributing disproportionately to low *M* values. We therefore repeated the analyses without these loci, which resulted in significantly low *M* values for the 1980 and 1994 samples assuming $\theta = 1.0$ and for the 1994 sample assuming $\theta = 4.0$. None of the *M* values were significant in the 2002 sample (Table 3). *M* values from the simulated samples of offspring of 20 and 50 parent fish were of the same magnitude as those observed in the empirical samples; when *C2-157* and *Cocl-Lav52* were omitted, *M* values were significant assuming $\theta = 1.0$, but not for $\theta = 4.0$ (Table 3).

Table 3. Results of tests for recent population bottlenecks based on *M* values (the ratio of the number of alleles to the allele size range; Garza and Williamson 2001).

	All loci		Excluded	
	$\theta = 1.0$	$\theta = 4.0$	$\theta = 1.0$	$\theta = 4.0$
Temporal data				
1980				
M	0.703		0.753	
P	0.002	0.018	0.026	0.143
1994				
M	0.658		0.706	
P	0.002	0.003	0.005	0.032
2002				
M	0.747		0.812	
P	0.012	0.086	0.117	0.424
Simulated data 2006, 20 parents				
M	0.702		0.748	
P	0.001	0.014	0.019	0.105
Simulated data 2006, 50 parents				
M	0.703		0.768	
P	0.002	0.017	0.037	0.180

Note: Four sets of analyses were conducted assuming θ values of either 1.0 or 4.0 and involving either all loci or excluding two loci with outlier alleles (*C2-157* and *Cocl-Lav52*). The analyses were conducted for each temporal sample from 1980 to 2002 and for the simulated samples representing recent population declines. The significance of *M* was tested using the software M_P_VAL (Garza and Williamson 2001).

Discussion

N_e of North Sea houting

We estimated N_e based on a temporal method that assumes a closed population (Beaumont 2003) (i.e., with no immigration from other populations). This is an important assumption, as immigration may bias N_e estimates if not accounted for in the method used (Wang and Whitlock 2003; see also Østergaard et al. 2003). It is likely that gene flow has occurred historically among North Sea houting populations. However, given that the Vidaa River at present is by far the largest population component and given that the few neighbouring populations most likely represent stocked Vidaa fish, we find it valid to assume a closed population.

The finding that the upper confidence limits increased with increasing N_{emax}, both using Beaumont's (2003) and Wang's (2001) methods, is not surprising. The point estimates of N_e were high, and by definition high N_e values re-

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sult in little drift and thereby a low signal:noise ratio, whereas low N_e values are much easier to estimate (Waples 1990). If a "traditional" F-based temporal method (Waples 1989) had been used, the upper confidence limits would have corresponded to infinity. The point estimate of N_e exceeds 500 irrespective of the method used, and based on the lower 90% HPD limit we conclude that N_e from 1980 to the present is unlikely to be lower than ~300 and could well be considerably higher. In the context of the "50-500 rule" (Franklin 1980), this means that N_e is clearly above the value of 50 recommended to avoid inbreeding depression in the short term, and presumably it also fulfils the requirement of N_e > 500 to ensure evolutionary potential in the long term. It should be noted, however, that the latter number has been subject to discussion, with some authors arguing that maintenance of evolutionary potential requires N_e >> 1000 (Lynch and Lande 1998; but see also reply by Frankham and Franklin 1998).

Is N_e declining or stable?

Even though N_e was found to be high, this does not show whether N_e is declining, stable, or even expanding; a very high N_e in 1980 and a low N_e in 2002 could result in a relatively high harmonic N_e over the time period. However, using the option in Beaumont's (2003) method for estimating N_e at the beginning and end of the sampled time interval suggested neither declines nor expansions. Consequently, we assume that N_e is both high and relatively stable over the time interval from 1980 to 2002.

In contrast with the results obtained using Beaumont's (2003) temporal method, Garza and Williamson's (2001) test for bottlenecks yielded significant outcomes for the 1980 and 1994 samples, even when two loci showing wide ranges of allele sizes and outlier alleles were omitted. One interpretation would be that a population decline had occurred prior to 1980, which could be detected in the 1980 and 1994 samples, whereas the signal was no longer evident in 2002. We are not aware of specific incidences that could have caused a bottleneck in the Vidaa River population before 1980, but perhaps the significant tests could reflect that this population was previously a part of a much larger system of North Sea houting populations connected by gene flow. Hence, the test could have detected a population decline from many thousands in the total subdivided population to a few hundreds or thousands in the current Vidaa River population after extirpation of the other populations. There is also the more simple explanation that some of the studied loci (in addition to the excluded loci *C2-157* and *Cocl-Lav52*) did not conform to the mutation model and parameters assumed in the test. Finally, it should be noted that the method does not perform well at small values of θ, which could compromise the results assuming a θ value of 1 (Garza and Williamson 2001).

Feasibility of genetic monitoring of N_e

Estimation of N_e at the beginning and end of the sampled time interval using Beaumont's (2003) method provided a powerful test for declining N_e, as evidenced by the results obtained from the simulated samples. The Bayes factor overwhelmingly supported the hypothesis of population decline for the simulated sample based on 20 parent fish, and there was also strong evidence for a decline in the sample based on offspring from 50 parents. However, the results of the simulated 50 parents case also showed that less drastic population declines (i.e., >50 parents) will yield Bayes factors <10, thereby providing none or only moderate statistical support for a population decline, at least given the sample sizes and number of loci used in this study. The simulated samples should be considered a rough approximation to a real population decline. In particular, the North Sea houting has overlapping generations, whereas our simulated samples reflect one discrete generation from 2002 to 2006. On the other hand, if the decline were consistent, then in a real population other cohorts in addition to that born in 2002 would also be expected to be affected. Nevertheless, the presence of a discrete generation from 2002 to 2006 may have introduced some bias causing the N_0 estimates to exceed the 20 and 50 parent fish assumed in the simulations.

In contrast with results obtained by the temporal method, Garza and Williamson's (2001) method did not provide strong evidence for a population decline in the simulated samples. Even the simulated samples based on 20 parents did not result in lower M values than were observed in the empirical samples. Clearly, a stronger bottleneck occurring over more generations would be required for a significant signal to occur, thereby making this method less useful for real-time management of North Sea houting. It should be mentioned that we also analysed the data using Cornuet and Luikart's (1996) BOTTLENECK test, which is supposed to be statistically less powerful than Garza and Williamson's method, and as expected we did not obtain significant signals of recent bottlenecks (data not shown).

Monitoring of population size in the Vidaa River North Sea houting has so far been conducted using electrofishing surveys. This approach has some drawbacks, including low efficiency at high water levels during the spawning time of North Sea houting in December–January and low numbers of recaptures, which results in very wide confidence intervals of census population size estimates. Estimates of N_e could in principle be used to estimate census population size (N), though this is not trivial (see Kalinowski and Waples 2002 for discussion). Given the wide confidence limits for the N_e estimates in the present study and the uncertainties associated with estimating N from electrofishing surveys, we would be hesitant to estimate N based on a fixed N_e/N ratio. Moreover, there are situations where the N_e/N ratio could change considerably over time, for instance if it was decided to reiterate a supportive breeding program in the Vidaa River. This could potentially lower the N_e but at the same time increase the census population size if a large fraction of the total population represents stocked fish based on a low effective number of parents (Ryman and Laikre 1991; Waples and Do 1994). Therefore, we do not see a genetic monitoring program as a replacement for electrofishing surveys, but rather as an important supplement that provides complimentary information based on independent data. It is now the intention to integrate genetic monitoring in the routine genetic monitoring program for North Sea houting, thereby providing information on both demographic and genetic risks to the future persistence of the species.

In conclusion, we found that the North Sea houting in the Vidaa River is not immediately threatened by inbreeding or loss of evolutionary potential. The most significant threat to

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the species is that only one major population component remains, rendering it highly vulnerable to catastrophic events, such as disease outbreaks or accidental pollution. Our results further show that Beaumont's (2003) method is very promising for routine genetic monitoring of effective population size. Numerous other examples can be found in the literature of isolated, endangered populations of freshwater fishes where similar genetic monitoring programmes could be conducted, such as the the Copper redhorse (*Moxostoma hubbsi*; Lippé et al. 2004), the Cape Fear shiner (*Notropis mekistocholas*; Saillant et al. 2004), and the marble trout (*Salmo marmoratus*; Fumagalli et al. 2002).

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Projected impacts of climate warming on production of lake trout (*Salvelinus namaycush*) in southern Yukon lakes

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Abstract: We used existing models to predict changes in lake surface temperature and thermocline depth, in combination with a newly developed model to describe lake thermal profiles, to determine how thermal properties of a series of lakes located predominantly in the southern Yukon could change under three realistic climate-warming scenarios. We then used existing models to determine how relative changes in potential harvest of lake trout (*Salvelinus namaycush*) in southern Yukon lakes could change as availability of optimal thermal habitat was altered under the three warming scenarios. With warming, an overall decrease in availability of optimal thermal habitat and in lake trout potential harvest is predicted in southern Yukon lakes, although considerable lake-specific variation in direction and magnitude of change exists. For southern Yukon lakes overall, 2, 4, and 6 °C increases in mean annual air temperature lead to 12%, 35%, and 40% decreases in thermal habitat volume, respectively, and 8%, 19%, and 23% reductions in potential harvest, respectively.

Résumé : Nous avons utilisé des modèles préexistants pour prédire les changements de la température de la surface des lacs et de la profondeur de la thermocline, en combinaison avec un nouveau modèle pour décrire les profils thermiques des lacs, afin de déterminer de quelle manière les propriétés thermiques d'une série de lacs situés en majorité au sud du Yukon pourraient être modifiées selon trois scénarios réalistes de réchauffement climatique. Nous avons ensuite utilisé des modèles préexistants pour déterminer comment la récolte potentielle de touladis (*Salvelinus namaycush*) dans les lacs du sud du Yukon pourrait changer à mesure que la disponibilité de leur habitat thermique optimal est modifiée selon les trois scénarios de réchauffement. Avec le réchauffement, on s'attend à une réduction globale de la disponibilité de l'habitat thermique optimal et de la récolte potentielle de touladis dans les lacs du sud du Yukon, bien qu'il existe une variation considérable du sens et de l'amplitude du changement en fonction des lacs. En général pour les lacs du sud du Yukon, des accroissements de la température annuelle moyenne de l'air de 2, 4 et 6 °C mènent à des réductions du volume de l'habitat thermique respectivement de 12, 35 et 40 % et des diminutions de la récolte potentielle de 8, 19 et 23 %.

[Traduit par la Rédaction]

Introduction

Fish are heterothermic ectotherms with body temperatures, for most species, within a few tenths of a degree of the water temperature in which they live; thus habitat temperature directly influences their physiology and behavior (Magnuson et al. 1990). Fish exploit specific ranges of water temperature, depending on species, age, and thermal history (Crawshaw and O'Connor 1996), and appear to have an innate desire to remain within a preferred range (Mac 1985). A species' behavioral thermal regulation is characterized by a narrow range of temperatures into which it will ultimately gravitate with all other variables being equal or nonrestricting (Christie and Regier 1988). This temperature is the species "final preferendum" (Fry 1947) and is included in the species fundamental thermal niche (Christie and Regier 1988), which, in turn, defines optimum conditions for activity and growth (Christie and Regier 1988; Magnuson et al. 1979). For lake trout (*Salvelinus namaycush*), a cold-water species with a natural distribution that is primarily dependent on the species' requirements for cold water and relatively high concentrations of dissolved oxygen (Martin and Olver 1980), the fundamental thermal niche is identified as 10 ± 2 °C (Magnuson et al. 1990). Investigations by O'Connor et al. (1981), as well as results of a literature search completed by Christie (1986), suggest that lake trout growth is optimal within this temperature range. Volume of water within this fundamental thermal niche has been established as a strong predictor of lake

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trout yield (Christie and Regier 1988) or potential harvest (Payne et al. 1990). For this species, thermal habitat volume (THV), which is the volume of water in a given lake within the preferred thermal range of 8–12 °C, was the best predictor of yield (or potential harvest) compared with thermal habitat area, lake area, lake volume, or other indices of thermal habitat availability (Christie and Regier 1988).

Climate warming is expected to alter the size of this thermal niche by changing annual patterns of thermal structure simultaneously with other changes in precipitation, cloudiness, windiness, and ice cover that would influence other niche characteristics of fish (Magnuson and DeStasio 1997). It is generally agreed that temperate zone fish with moderate to high preferred temperatures should benefit (e.g., increased productivity) from climate warming through increased availability of thermal habitat in more northerly areas (Magnuson and DeStasio 1997; Shuter and Post 1990). Lake trout, on the other hand, will likely experience reduced availability of their preferred thermal habitat, particularly at the southern extent of their range, coupled with reductions in production (Meisner et al. 1987; Shuter and Meisner 1992; Shuter and Lester 2004) as lakes warm.

Climate-warming models predict greater warming at increasingly northern latitudes, yet existing lake-warming models are not able to quantify the magnitude of these changes on northern lake systems because they are calibrated to more southerly conditions where adequate meteorological data exist. For example, DeStasio et al. (1996) used the DYRESM model of Imberger and Patterson (1981, 1990), McCormick (1990) used Garwood's (1977) model, and the MINLAKE model of Riley and Stefan (1988) and Hondzo and Stefan (1993) was developed from a Minnesota data set. With the above models, it is often assumed that results can be extrapolated spatially because of the lack of topographic complexity in the region of study (e.g., MINLAKE model based on Minnesota data) and the relative lack of variability in meteorological conditions over vast distances. In the north, however, extensive meteorological data are often lacking (e.g., detailed wind-speed data at local scales), and in mountainous regions, considerable localized variation in meteorological conditions exists, rendering these models unreliable. Although it is difficult to predict impacts of climate warming with certainty, the approach taken here is an attempt to predict how warming could influence lake thermal characteristics of a subset of northern lakes, without the luxury of localized meteorological data.

The objectives of this study include development of a method to describe current lake thermal profile characteristics and approximate how thermal properties could be affected by climate warming given limited availability of both meteorological and lake thermal data for northern lakes. We then estimated current availability of lake trout thermal habitat and changes in habitat availability under increasing mean annual air temperatures. Finally, we estimated changes in lake trout potential harvest (Payne et al. 1990) under a series of warming scenarios using established relationships. These simulations allow estimation of both lake-specific and regional impacts of climate warming on potential harvest of northern lake trout populations.

Materials and methods

Study lakes

Potential effects of climate warming on lake thermal characteristics were evaluated from a data set of 33 Yukon lakes of various morphometries (Table 1), located predominantly in the southwestern portion of the Territory (Fig. 1) between 59°N and 63°N latitude. We included only lakes for which a midsummer thermal profile (late July to early August) and a previously digitized bathymetric map in geographic information system (GIS) format existed. When multiple profiles were available for a lake, the deepest was used in the analyses. All lake temperature data were collected with a regularly calibrated Datasonde 3 Hydrolab with Scout 2 (Hydrolab Corporation, Austin, Texas). The data set of lakes fitting the criteria for inclusion in this study is relatively representative of Yukon lake trout lakes in general (for which data exist) in terms of lake volume (Fig. 2*a*) and lake area (Fig. 2*b*). It should be recognized, however, that this is a small sample of all Yukon lakes, the majority of which have had no thermal or morphometric information previously collected.

Thermal habitat volume

To calculate thermal habitat volume (THV) for lake trout, it was necessary to describe current lake thermal profiles to determine the depth at which the upper (12 °C) and lower (8 °C) boundaries of lake trout optimal habitat occur, determine lake area at boundary depths, and subsequently calculate the volume of water in each lake within the optimal thermal range. To describe lake thermal characteristics in all lakes in which a thermocline was apparent, the shape of each lake thermal profile was described by

$$(1) \qquad T = T_b + T_d(D^{STEEP}/Z_{th}^{STEEP} + D^{STEEP}))$$

where T is the temperature (°C) at a given depth, T_b is the bottom temperature (°C) of the lake (profile), T_d is the difference in temperature from the surface to the bottom (i.e., $T_d = T_{surface} - T_b$) of the profile, D is the given depth (m) in the profile, Z_{th} is the thermocline depth (m), and STEEP is a unitless parameter describing the degree of isothermality of the epilimnion (and hypolimnion) given the symmetrical nature of the function and describes the sharpness of the thermocline. The equation is a three-parameter sinusoidal function in which a constant parameter (T_b) has been added to ensure a non-zero intercept, with variable steepness (rate of temperature change) between high and low asymptotes. Equation parameters were fit using the SOLVER tool in Microsoft Excel® to achieve the closest fit to the empirical thermal profile by minimizing the sum of squared residuals. When SOLVER gave a negative (or <4) value for T_b, the T_b was set to 4 °C to ensure biologically reasonable parameter values. Equation 1 was solved at 8 and 12 °C (T) to determine the depth (D) at which these temperatures occurred.

Before volume calculations, it was necessary to calculate lake area at each of the optimal thermal habitat boundaries. An adjustment of the interpolation equation suggested by

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Table 1. Climatological, thermal, and morphological characteristics of 33 southern Yukon lake trout (*Salvelinus namaycush*) lakes.

	Latitude	Longitude	Surface area (km^2)	FT (km)	Maximum depth (m)	$\bar{Z}$ (m)	TEMP (°C)	HRISE (°C)	THMZ (m)	Thermal group
Alligator	60°23′N	135°21′W	6.3	5.7	10	5.6	–1.4[a]	13.3	n/a	G1
Atlin	60°00′N	133°50′W	634.5	65.8	250	78.9	–2[a]	14.6 (13.2)	26.2 (22.3)	G4
Bennett	60°06′N	134°52′W	96.8	24.5	120	61.1	–1.4[a]	10.4 (10.0)	29.4 (30.5)	G2
Chadburn	60°03′N	134°57′W	1.9	2.2	42	14.5	–0.7[b]	16.1 (16.2)	9.8 (10.2)	G4
Dezadeash	60°28′N	136°58′W	82.5	19.5	6	4.1	–2.9[b]	17.3	n/a	G1
Ethel	63°22′N	136°06′W	47.3	18.8	60	30.7	–3.6[b]	14.4 (14.6)	9.9 (11.3)	G4
Fish	60°36′N	135°14′W	13.2	9.9	35	16.9	1[b]	15.9 (15.8)	9.5 (10.2)	G3
Fox	61°14′N	135°28′W	16.6	16.5	45	28.9	1[b]	19.6 (19.3)	9.9 (12.0)	G4
Frederick	60°23′N	136°40′W	4.5	6.4	40	22.3	–2.9[b]	14.6 (14.6)	13.5 (14.0)	G4
Granite	60°42′N	137°05′W	1.7	3.8	55	37.2	–2.9[b]	13.5 (13.6)	12.9 (13.6)	G4
Howard (N)	60°14′N	136°49′W	2.0	2.8	16	6.0	–2.9[b]	13.9 (13.6)	14.3 (14.0)	G3
Hutshi	61°08′N	136°35′W	3.2	4.2	16	5.0	–4.4[a]	15.5	n/a	G1
Jojo	60°34′N	136°21′W	6.4	9.3	60	28.3	–2.9[b]	12.0 (11.9)	19.6 (22.7)	G2
Kathleen	60°28′N	136°58′W	33.8	11.1	108	54.5	–2.9[b]	10.0 (9.8)	43.4 (43.0)	G2
Klukshu	60°19′N	136°59′W	1.5	3.1	30	13.3	–2.9[b]	13.0 (12.7)	17.6 (21.7)	G4
Kusawa	60°20′N	136°22′W	142.0	22.1	140	54.4	1[b]	16.5 (16.6)	25.9 (15.1)	G4
Laberge	61°11′N	135°12′W	201.0	50.2	140	52.9	1[b]	19.5 (18.0)	n/a (18.9)*	G4
Lewes	60°22′N	134°50′W	1.4	2.5	40	16.8	1[b]	15.3 (15.3)	14.1 (14.2)	G4
Little Atlin	60°15′N	133°57′W	37.9	15.3	45	11.0	1[b]	17.4 (16.7)	12.3 (12.9)	G3
Little Braeburn	60°30′N	135°49′W	0.8	1.9	40	12.8	–3.8[b]	17.2 (17.3)	7.1 (7.9)	G4
Little Fox	61°20′N	135°38′W	2.2	2.2	35	17.1	1[b]	17.2 (17.0)	7.6 (7.7)	G4
Little Salmon	62°11′N	134°40′W	62.1	28.8	140	93.1	–2.9[a]	14.7 (14.1)	16.0 (9.5)	G4
Long	61°21′N	136°41′W	13.9	9.4	50	16.8	–4.4[a]	10.2 (10.2)	28.1 (29.2)	G2
Louise (Jackson)	60°42′N	135°17′W	0.5	1.2	10	6.2	–2.9[b]	16.1 (16.1)	7.7 (8.2)	G3
Lower Snafu	60°11′N	133°26′W	2.9	1.5	25	5.9	–2[b]	17.0 (17.3)	9.4 (7.8)	G4
Marsh	60°25′N	134°18′W	96.3	22.3	50	12.8	1[b]	16.4 (15.6)	22.2 (22.2)	G3
Pine	60°49′N	137°27′W	5.5	5.7	25	14.9	–2.9[b]	15.6 (15.4)	12.4 (12.7)	G4
Tagish	60°10′N	134°20′W	354.6	31.6	300	61.2	1[b]	13.3 (13.3)	22.9 (25.2)	G4
Tarfu	60°03′N	133°43′W	4.2	4.3	30	11.9	1[b]	16.0 (15.7)	10.3 (10.6)	G4
Teslin	60°15′N	132°57′W	354.0	54.5	213	54.1	–2[b]	14.4 (14.0)	22.9 (21.9)	G4
Tincup	61°45′N	139°15′W	17.9	9.5	180	101.9	–4[b]	13.9 (14.3)	6.8 (8.3)	G4
Twin	61°42′N	135°55′W	1.6	1.8	40	16.3	–3.8[b]	18.7 (18.9)	7.0 (7.4)	G4
Wellesley	62°21′N	139°49′W	73.8	14.7	45	23.6	–6.3[a]	15.9 (15.8)	15.8 (16.4)	G4

Note: FT, lake fetch (km); $\bar{Z}$, mean depth of lake (m); TEMP, long-term mean annual air temperature (°C); HRISE, maximum summer surface temperatures (°C); THMZ, thermocline depth (m); asterisk (*) indicates reference to Mackenzie-Grieve (2005); n/a, not applicable. For each lake, the initial value in the HRISE and THMZ columns is the empirical measurement and the value in parentheses is that predicted by the relevant equation.

[a]TEMP from Canadian climate normals for 1951–1980.

[b]TEMP from Canadian climate normals for 1961–1990.

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Fig. 1. The majority of the lakes included (n = 33) are located in the southern Yukon, Canada, and range from 59°N to 63°N latitude. Approximate locations of individual lakes are indicated by **X**. Major highways are indicated on the map.

Payne et al. (1990) was used (the area measurement was substituted for the temperature measurement) where

$$(2) \qquad A_t = A_1 + ((D_t - D_1)(A_2 - A_1)/(D_2 - D_1))$$

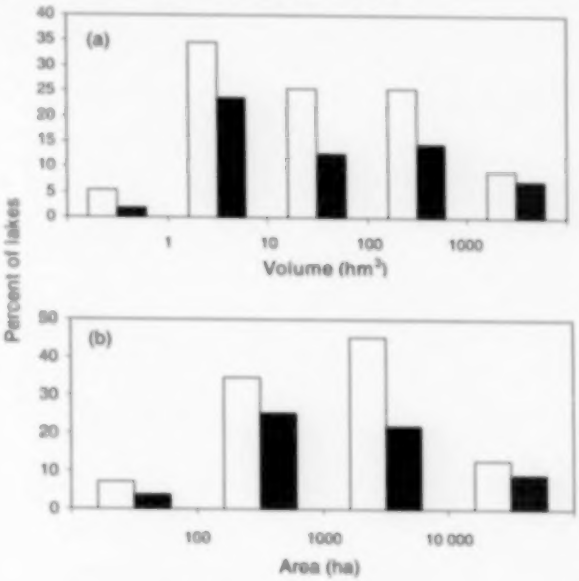
The equation was solved for A_t (area at either 8 °C or 12 °C) (km^2), where D_t is the depth (km) at either 8 °C or 12 °C, A_1 is the area (km^2) closest to, but greater, than A_t, A_2 is the area (km^2) closest to, but less than, A_t, D_1 is the depth (km) at A_1, and D_2 is the depth (km) at A_2. Areas of A_1 and A_2 were determined from bathymetric maps.

The volume (V) of habitat in a lake within the optimal thermal range for lake trout was calculated as follows, according to Welch (1948):

$$(3) \qquad V = (h/3)\left(A_1 + A_2 + \sqrt{A_1 \cdot A_2}\right)$$

where h is the vertical depth of the stratum (km), A_1 is the area of upper surface (km^2), and A_2 is the area of the lower of the lower surface of the stratum (km^2). Island volumes were subtracted from the water volume (as calculated above) to obtain an estimate of total volume of optimal lake trout habitat (THV) in each lake.

Fig. 2. Study lakes are reasonably representative ((*a*) by volume (1 hm^3 = 0.001 km^3) and (*b*) by surface area) of Yukon lake trout (*Salvelinus namaycush*) lakes overall (for which data exist). Study lakes include about 60% of all lake trout lakes for which data are available from Yukon Government files (all lakes, n = 55, open bars; study lakes, n = 33, solid bars).



Lake trout production

Current lake trout potential harvest was estimated following Payne et al. (1990) where July THV was related to potential harvest by

$$(4) \qquad \log_{10} H = 2.15 + 0.714 \log_{10}(\text{July THV})$$

where H is the potential harvest (kg·year^{-1}) and July THV (hm^3) (1 hm^3 = 0.001 km^3) is the thermal habitat volume calculated from July temperature data only.

Payne et al. (1990) developed eq. 4 by linear regression of the original 15 lakes used by Christie and Regier (1988) plus an additional five lakes with surface areas less than 60 km^2 (6000 ha). The Payne et al. (1990) equation was used in our analyses as the majority of Yukon lakes included here are less 60 km^2 (Table 1). Payne et al. (1990) also found that using a geometric average of July THVs, rather than the 10-day summer averages used by Christie and Regier (1988), improved the precision of the model. We assumed that a single-lake July or early August thermal profile was representative of average July temperatures in a given lake.

Climate warming

Climate warming models predict mean annual surface air temperature increases of between about 2 °C and 5 °C by the year 2100 in the southwestern Yukon (http://www.cccma.bc.ec.gc.ca/eng_index.shtml). We evaluated the effect of climate warming on lake thermal characteristics under three different temperature scenarios: current mean annual air temperature at each of the lakes was increased by 2, 4, and

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6 °C. We assumed that mean annual air temperature was the driver of changes in lake thermal profiles with climate warming. We assumed that these changes incorporated the mechanics of lake warming explicitly considered in other, more-complicated lake-warming models (e.g., Hondzo and Stefan 1993).

Shuter et al. (1983) used mean annual air temperature, lake mean depth, and lake fetch to determine thermocline depth according to

$$\ln(\mathrm{THMZ}) = 0.220\ln(\mathrm{FT}) + 0.213\ln(\bar{Z}) - 0.0263(\mathrm{TEMP}) + 1.550 \quad (5)$$

where THMZ is the thermocline depth (m), FT is lake fetch (km), $\bar{Z}$ is the mean depth of lake (m), and TEMP is the long-term mean annual air temperature (°C). Data from a wide latitudinal range (41°N–75°N latitude) were included in the analyses used to develop these predictive equations and should therefore be appropriate for use here where latitudes of database lakes range from 59°N to 63°N latitude. Hanna (1990) suggested that of the 17 models of mixing depth that she evaluated, the Shuter et al. (1983) model, although slightly biased (overestimates thermocline depth), was the best available for predicting mixing (thermocline) depth.

Shuter and Post (1990) used mean annual air temperature (TEMP; °C) and mean depth ($\bar{Z}$; m) to predict maximum summer surface temperatures (HRISE; °C) according to

$$\log_e(\mathrm{HRISE}) = 0.0437(\mathrm{TEMP}) - 0.002(\mathrm{TEMP})^2 - 0.108\log_e(\bar{Z}) + 3.158 \quad (6)$$

To assess how climate warming (i.e., increase in TEMP) impacts lake thermal characteristics, $T_{surface}$ ($T_d = T_{surface} - T_b$) and Z_{th} parameters of the sinusoidal function fitted to observed data were adjusted by the difference in values predicted by the above equations with increases in TEMP from current conditions. For example, if the HRISE ($T_{surface}$) predicted under current climatic conditions was 15 °C and the HRISE predicted under a 2 °C increase in mean annual air temperature was 17 °C, then the value of the T_d parameter of the sinusoidal function was increased by 2 °C from the current fitted value. The sinusoidal equation (eq. 1) was then resolved at depths in the original profile to allow comparison of lake thermal profiles under the various climate warming scenarios. We assumed that increases in TEMP would have little effect on T_b, consistent with results of other lake-warming models (Hondzo and Stefan 1993; Stefan et al. 1993). We also assumed that neither the STEEP parameter in eq. 1 nor $\bar{Z}$ and FT in eqs. 5 and 6 would change under climate warming.

Although THV for each of the study lakes under climate warming was calculated as previously described for current lake thermal profiles, we interpreted changes in potential harvest in terms of relative percent changes because lake productivity in northern regions is generally lower than in southern regions (where the majority of the data on which the equation was based originates).

Three of the study lakes were approximately isothermal based on their midsummer profiles. Although there were small temperature differences in lake surface and bottom temperatures (<2 °C), we assumed that surface temperature was representative of average lake temperature. For these three lakes, maximum surface water temperature under increased TEMP was calculated using eq. 6. Current maximum surface temperatures were then adjusted by the difference between equation predictions and current conditions. Potential harvest calculations were not performed as no appreciable volume of optimal thermal habitat currently exists in any of these three lakes.

Results

Thermal profiles and habitat volume

The 33 Yukon lake trout lakes were divided into four groups based on lake thermal properties (Fig. 3): group 1 ($n = 3$), lakes where there is currently no thermal habitat in the main basin of the lake (i.e., lakes are isothermal); group 2 ($n = 4$), lakes where there is currently no water warmer than the upper optimal thermal limit for lake trout of 12 °C; group 3 ($n = 5$), lakes where there is currently no habitat colder than the lower optimal thermal boundary of 8 °C; and group 4 ($n = 21$), lakes where there is currently water colder and warmer than the lower (8 °C) and upper (12 °C) optimal thermal boundaries for lake trout.

The sinusoidal function used to describe characteristics of lake thermal profiles provided a good fit to most of the lake data, although the fit was poorer in lakes with secondary (temporary) thermoclines or where the epilimnion was less well mixed (e.g., surface warming on a warm, calm day). There were generally only small differences in fitted versus empirical thermocline depths and surface temperatures (Table 1). The fitted thermocline depth (eq. 1) did slightly overestimate empirical thermocline depth, although differences were usually less than 0.5 m. Any differences in fitted and empirical surface temperatures (eq. 1) were almost always less than 0.5 °C. These model fits provided the template for current thermal profiles to which warming scenarios were applied.

In the 30 Yukon lakes in which thermoclines were identified (groups 2, 3, and 4), thermocline depth became increasingly shallow with increasing TEMP, although the magnitude of the surfaceward shift was not the same for each 2 °C increase in TEMP. As the thermocline was shifted up in the water column with increases in TEMP, optimal thermal habitat boundary depths also shifted in the water column, although neither the direction of change (i.e., up or down in the water column) nor the changes in THV were consistent across all lakes.

Group 1 lakes (nonstratified) currently have no appreciable volume of midsummer optimal habitat (Table 2). With increases in TEMP, average lake temperatures in the warmest part of the summer further increased, pushing temperatures even further beyond the optimal range for lake trout throughout the warmest part of the year.

Group 2 included some of the larger, colder lakes in the southern Yukon, where there was currently either no 12 °C isotherm or this isotherm was at the lake surface. In lakes of this type, THV generally decreased slightly with a 2 °C increase in TEMP (Table 2). In two of the four lakes, slight increases in THV were predicted, and in the other two lakes,

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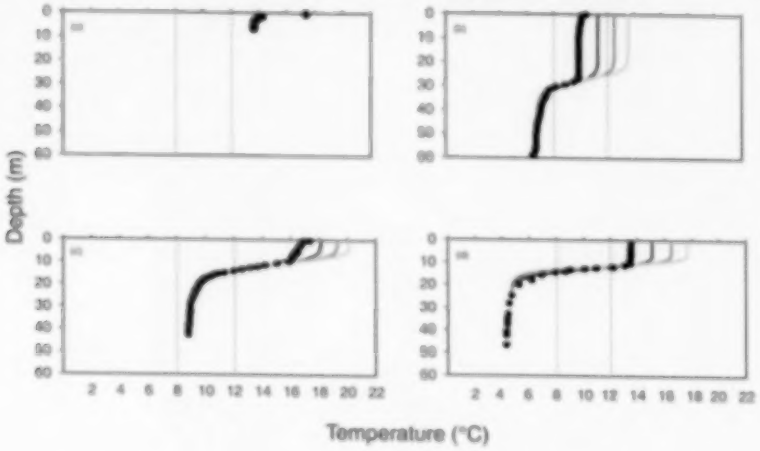
Fig. 3. Empirical and temperature measurements, fitted thermal profiles, and warmed midsummer thermal profile of four Yukon lakes typical of each of the four groups of lakes based on spatial patterns of lake trout (*Salvelinus namaycush*) thermal habitat volume as defined by habitat between 8 and 12 °C (indicated by dotted vertical lines). (*a*) Thermal group 1 ($n = 3$); (*b*) group 2 ($n = 4$); (*c*) group 3 ($n = 5$); and (*d*) group 4 ($n = 21$). See text for details on thermal groups. Solid circles indicate empirical data; lines indicate the current fitted profile, dark shaded lines indicate the predicted profile under a +2 °C increase in mean annual air temperature, medium shaded lines indicate the +4 °C profile, and light shaded lines indicate the +6 °C profile.



decreases in THV were predicted (Table 2). With 4 °C and 6 °C increases in TEMP, large reductions in THV occurred (Table 2) as the 12 °C isotherm developed (generally with a 4 °C increase in TEMP) deep in the water column, leading to an overall reduction in THV in these lakes through vertical compression of the extent of lake trout habitat.

In group 3 lakes, no 8 °C isotherm currently existed as lake temperatures exceeded 8 °C in midsummer. The THV predictions for these lakes varied little with increases in TEMP compared with lakes of groups 2 and 4 (Table 2) as there was little change in the position of the 12 °C isotherm. With a 2 °C increase in TEMP, a reduction in mean THV of only 6% was predicted, whereas under a 6 °C TEMP increase scenario, a slight increase in the mean THV (1.2%) was predicted compared with current conditions. Increases in THV were predicted for four of the five lakes of this type. Little change in THV occurs in these lakes because lake warming occurs in the epilimnion of the lakes and the 12 °C isotherm in group 3 lakes is deeper and therefore less affected by surface warming.

With increases in TEMP, THV in the group 4 lakes (where 8 °C and 12 °C isotherms currently exist) was compressed as the dimension (height) of the optimal habitat layer decreased in all cases, resulting in a decrease in THV with increasing TEMP. The majority of lakes in our data set are of this type (21 of 33). The optimal thermal habitat is almost always a small proportion of total lake volume (Table 2) and is generally restricted to the metalimnetic region in these lakes. The compression of THV in group 4 lakes occurs by one of two mechanisms. Thermal habitat is reduced either by a deepening of the 12 °C isotherm combined with a shallowing of the 8 °C isotherm or by a shallowing of the 12 °C isotherm combined with a shallowing of the 8 °C isotherm. In the latter case, the magnitude of the shallowing of the 8 °C and 12 °C isotherms (and associated increase in lake area at depth) is not enough to counter the reduction in height of the optimal thermal habitat layer, thus results in an overall decrease in THV. Specifically, under a 2 °C increase in TEMP, an average 13% reduction in THV occurred, and under a 4 °C increase in TEMP, an average 20% reduction in THV occurred, whereas under a 6 °C increase in TEMP an average reduction in THV of 27% is expected (Table 2).

Pooling all data for the southern Yukon lakes database for each of the three warming scenarios suggested an overall decrease in THV for lake trout in Yukon lakes, where magnitude of the decrease in THV was greater with increasing changes in TEMP. With a 2 °C increase in TEMP, a mean 12% decrease in THV was predicted, and with a 6 °C increase in TEMP, more than a 40% decrease in THV was predicted (Table 2).

Warming and lake trout potential harvest

In group 1 lakes, no appreciable volume of preferred thermal habitat currently exists. We assumed, as in the other lakes, that the late July – early August profile was representative of July thermal habitat conditions and therefore related to potential harvest by the Payne et al. (1990) equation. With essentially no optimal thermal habitat in group 1 lakes, the Payne et al. (1990) equation could not be applied. Lake trout production in lakes of this type is probably already limited by elevated water temperatures.

In group 2 lakes, there was a small overall average decrease in H by 12% with a 2 °C increase in TEMP. This overall decrease was the result of a large decrease in H in a single lake, as other lakes in this group actually showed small increases or decreases in H. As TEMP further increased, large decreases in H resulted in all cases. With a 4 °C increase in TEMP, an average decrease of 61% was predicted, and with a 6 °C increase in TEMP, an average decrease of 67% was predicted (Fig. 4).

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Table 2. Current and predicted changes in July thermal habitat volume (THV) for 33 southern Yukon lake trout (*Salvelinus namaycush*) lakes under warming scenarios where current mean annual air temperature was increased by 2, 4, and 6 °C.

Lake	Total lake volume (hm^3)	Current July THV (hm^3)	Predicted change in July THV (%) with 2 °C increase	with 4 °C increase	with 6 °C increase
Group 1					
Alligator	34.0	—	—	—	—
Dezadeash	337.0	—	—	—	—
Ifutshi (S)	17.0	—	—	—	—
Group 2					
Bennett	5 990.0	2 514.7	–0.6	–81.8	–86.2
Jojo	196.0	132.6	–67.9	–73.3	–75.9
Kathleen	1 864.0	1 110.3	1.7	–82.4	–87.5
Long	259.0	189.7	10.5	–52.9	–65.1
Average			–14.1	–72.6	–78.7
Group 3					
Fish	218.0	120.8	–2.2	–1.6	0.7
Howard (N)	15.0	1.0	–6.7	–0.7	10.3
Little Atlin	402.0	140.6	1.2	4.3	8.8
Louise (Jackson)	4.0	0.3	–7.4	–4.5	4.9
Marsh	1 220.0	98.2	–14.9	–19.7	–18.9
Average			–6.0	–4.4	1.2
Group 4					
Atlin	54 400.0	6 290.9	–18.3	–28.2	–34.9
Chadburn	28.0	1.4	–3.2	–9.8	–16.4
Ethel	1 462.0	168.3	–16.0	–26.4	–34.3
Fox	475.0	72.4	–6.8	–12.8	–18.4
Frederick	101.0	10.5	–15.2	–24.0	–30.0
Granite	66.0	3.9	–21.1	–32.3	–39.4
Klukshu	0.0	7.2	–36.4	–49.4	–56.0
Kusawa	7 668.0	1 781.7	–5.4	–6.5	–12.0
Laberge	10 800.0	1 523.4	–6.3	–11.9	–17.0
Lewes	23.0	1.4	–8.5	–13.1	–16.9
Little Braeburn	11.0	1.0	–9.7	–16.6	–22.0
Little Fox	24.0	0.9	–8.6	–14.7	–19.6
Little Salmon	5 750.0	208.8	–18.2	–29.3	–37.4
Lower Snafu	18.0	1.0	–7.7	–11.9	–14.2
Pine	81.0	10.5	–7.3	–11.8	–15.0
Tagish	21 800.0	2 866.4	–16.8	–25.1	–30.2
Tarfu	49.0	3.4	–9.2	–14.7	–18.3
Teslin	20 800.0	1 461.6	–16.9	–26.7	–33.4
Tincup	1 844.0	72.5	–19.8	–34.5	–46.8
Twin	26.0	2.0	–8.8	–16.0	–22.2
Wellesley	1 757.0	233.3	–12.0	–20.0	–25.8
Average			–13.0	–20.7	–26.7
Yukon total[a]	137 351.0	26 376.7	–11.90	–34.50	–40.2

Note: Dash (—) indicates that THV is absent.
[a]Yukon total does not include group 1 lakes.

Our analyses suggest the impact of climate warming on the group 3 lakes will be minimal; slight increases in *H* are predicted in some lakes under the various levels of climate warming and slight decreases in *H* are predicted in others. Our analyses suggest that any increases in *H* will be less than 6% and any decreases will be less than 15% of the current *H* (Fig. 4). Our analyses predict that an increase in TEMP of 2 °C would lead to the greatest overall reduction in *H* (4.4%). When TEMP was increased by 4 °C, a 3.3% reduction in *H* in group 3 lakes resulted, whereas under a 6 °C increase in TEMP, an increase in *H* of 0.7% resulted (Fig. 4), with slight increases occurring in four of five lakes.

In group 4 lakes, decreases in *H* are predicted under all three warming scenarios, and the magnitude of these reduc-

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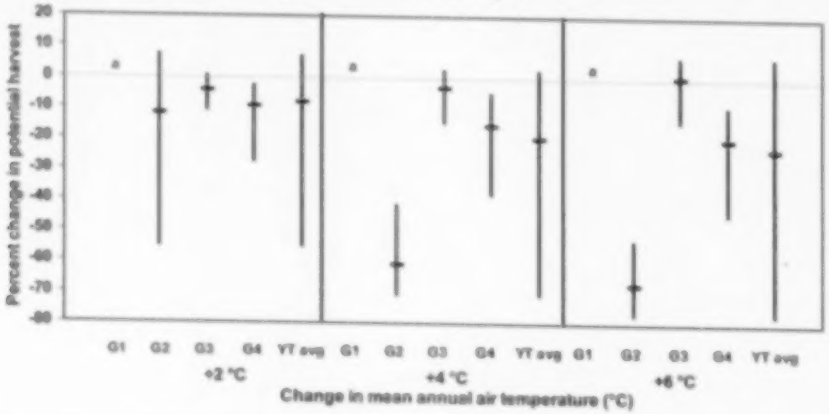
Fig. 4. Predicted percent change in lake trout potential harvest (*H*) for 33 Yukon lake trout (*Salvelinus namaycush*) lakes with increasing mean annual air temperature. Mean (short horizontal bars) and range (vertical bars) in percent change in *H* for each of the thermal groups under the applied climate warming scenarios are indicated: G1 (n = 3), lakes in which there is currently no optimal thermal habitat (i.e., "a"); G2 (n = 4), lakes in which there is currently no thermal habitat beyond the upper optimal thermal boundary; G3 (n = 5), lakes in which there is currently no thermal habitat colder than the lower optimal thermal boundary; and G4 (n = 21), lakes in which 8 and 12 °C isotherms currently exist. YT avg, Yukon Territory averages.



tions increased with increasing TEMP. For example, under a 2 °C increase, *H* decreased by 9.5% on average, under a 4 °C increase in TEMP, *H* decreased by a little more than 15% on average, and under a 6 °C increase in TEMP, *H* decreased by about 20% on average (Fig. 4).

Overall, lake trout potential harvest in southern Yukon lakes is expected to decrease with increasing TEMP. Under increases in TEMP of 2, 4, and 6 °C, mean decreases in *H* of about 8%, 19%, and 23%, respectively, are expected (Fig. 4).

Discussion

Probably the most important physical characteristic of a lake is its seasonal stratification pattern (Stefan et al. 1993). Application of the Shuter et al. (1983) model, which uses lake fetch, lake mean depth, and local mean annual air temperature to predict thermocline depth, shows that thermocline depth will become increasingly shallow with increasing mean annual air temperature. The directional change in thermocline depth as a result of climate change is equivocal in the literature, although predictions of our study are consistent with empirical data for Lake Opeongo (King et al. 1999) and Lake Huron (King et al. 1997) where shallower thermoclines have been associated with warmer climatic conditions. The greater density difference between surface and bottom water with increased surface layer warming is responsible for this stratification pattern. The shallower, stronger stratification predicted for lakes in our Yukon database is consistent with results of DeStasio et al. (1996) for small north-temperate lakes, Magnuson et al. (1990) for the Great Lakes, and McCormick (1990) for Lake Michigan, assuming that little change in wind energy occurs with climate warming.

Thermocline depth is relevant in the discussion of lake trout thermal habitat because optimal habitat is often restricted to this metalimnetic zone, particularly in our group 4 lakes, which were the most common lake type in our data set. The stronger stratification (i.e., increased thermal gradient) predicted under climate warming and predicted for our group 2 and group 4 lakes, in particular, implies a reduction in the vertical extent of the thermal niche during the summer stratification period. Our results are consistent with the a priori expectations of Magnuson et al. (1990) where this squeeze on the thermal niche was expected to increase (and affect habitat availability for lake trout more negatively) with climate warming, although their results did not support it. The group 3 lakes are less affected by changes in the depth and the strength of the thermocline because optimal habitat in these lakes is normally deep in the hypolimnion where changes in the upper lake profiles have little impact on temperatures near the bottom of these lakes.

In contrast to southern lakes in which lake trout are often restricted to metalimnetic and hypolimnetic areas in an effort to remain within the optimal thermal range (Ryan and Marshall 1994), the epilimnion of northern lake trout lakes is currently often within the optimal range for lake trout, as in our group 2 lakes. Under climate warming, however, our results suggest optimal habitat availability in northern lake trout lakes may further resemble that in southern lake trout lakes as temperatures in the epilimnion warm above 12 °C, leading to a vertical compression in optimal habitat as suggested by analyses on our group 2 lakes.

Hypolimnetic oxygen depletion has been less of a concern in northern systems compared with southern ones as lake trout are not usually restricted to this zone as in southern lakes. Dissolved oxygen (DO) concentrations rarely limit availability of optimal habitat for lake trout in northern lakes because temperatures are cold and lakes are usually oligotrophic. In our data set, DO concentrations of less than 6 $mg \cdot L^{-1}$, which is often considered to be the lower DO limit for optimal lake trout habitat (MacLean et al. 1990), occurred in the hypolimnion of only one basin in each of two lakes.

Under climate warming, oxygen depletion is expected to be of increasing concern in northern waters. Higher lake temperatures would result in reduced DO saturation values

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(Blumberg and DiToro 1990). The likely increases in primary production with warmer water temperatures (Rouse et al. 1997) increase the potential for summer oxygen depletion (Marshall 1996). Longer periods of stratification and more stable systems predicted from several models (DeStasio et al. 1996; Hondzo and Stefan 1993; Stefan et al. 1993) and observed in northern Ontario (Ryan and Marshall 1994) show that this will also lead to more pronounced oxygen depletion, increasing the frequency of anoxia in bottom waters in mid- and late summer and reducing DO habitat availability for lake trout. Such changes would place marginal populations at increased risk of population adverse processes.

A habitat model for lake trout developed by Dillon et al. (2003) used this DO concentration of 6 $mg \cdot L^{-1}$ as the lower optimal habitat boundary, whereas we employed the thermal measure (8 °C). The Dillon et al. (2003) model used data on lake morphometry, total phosphorus (TP) concentration, and secchi depth (or dissolved organic carbon concentration) to predict depth of the upper boundary of lake trout optimal habitat (10 °C isotherm) and depth of the lower habitat boundary as described above. Although this model is useful in estimating optimal habitat volume for lake trout in some cases, it was not the best model given our study objectives. Specifically, data on TP and secchi depth are not readily available for several lakes in our data set. Also, the optimal habitat volume as defined by Christie and Regier (1988) and by Payne et al. (1990) was strongly linked to measures of lake trout production, whereas the Dillon et al. (2003) model was not.

Of particular concern to Schindler (1997) when considering effects of climate warming on lake trout and other cold stenotherms was their presence in cold monomictic lakes with no summer thermal refugia. The shallow nature of these lakes predisposes them to warmer summer conditions and the optimal thermal habitat restrictions that follow. Although there is suitable thermal habitat in the spring and fall, the duration of "no thermal habitat" conditions in the summer is likely to increase with climate warming. Schindler (1997) suggested that for lakes that are isothermal in midsummer, even a temperature increase of a few degrees could lead to population extirpation of cold-water species such as lake trout. Localized extirpations of lake trout populations as a result of limited optimal summer habitat have already been reported in a number of lakes in central and eastern Ontario (MacLean et al. 1990).

Our analysis of changes to lake trout habitat volumes under reasonable warming scenarios suggests that climate warming will render most southern Yukon lakes less suitable for lake trout, resulting in overall decreases in potential harvest. Analyses by Minns and Moore (1992) suggest that the areas currently supporting the highest fish yields will become the areas with low or marginal yields under climate change and areas with the highest yields will be relocated northward. Our analyses, which have been restricted to southern Yukon lakes (because of limited data available for more northerly lake trout lakes), suggest that any increase in species productivity will be further north than the southern Yukon. Under climate warming, cold-water species such as lake trout would be restricted to lakes that are further north or at higher altitudes than where populations are currently found; an 8° shift in latitude or a 1500 m shift in altitude is predicted (McLain et al. 1994). Overall range shifts for lake trout are also likely in the long term, provided previously unusable habitat becomes accessible.

As with any modeling exercise, the validity of our results depends on the realism of the assumptions made in our models and the quality of the data used in the simulations. Even though there are uncertainties involved in predicting the magnitude of climate change, managers of renewable resources, including fisheries, must assess the scope of potential impacts of global warming and prepare for a range of future conditions (Minns and Moore 1992). This study provides a framework for continued analyses of these possibilities and identifies southern Yukon lake trout populations and lake types that could be at the greatest risk from climate warming in terms of preferred habitat reductions and subsequent decreases in lake trout potential harvest and population viability. The importance of enhanced data collection in Canada's north is clear, as according to ideas initiated by Minns and Moore (1992), potential harvest in Canada's far north should increase compared with current conditions.

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Historical changes in abundance and community structure of warmwater piscivore communities associated with changes in water clarity, nutrients, and temperature

M.M. Robillard and M.G. Fox

Abstract: In this study, we assess changes in the piscivore community of four large, shallow lakes in the Kawartha Lakes region of central Ontario, Canada, over the period from 1980 to 2003 and relate these changes to temporal trends in phosphorus concentration, water clarity, and temperature. Over the 24-year period of data collection, there has been a regional-scale decline in the relative abundance of walleye (*Sander vitreus*) and an increase in the relative abundance of bass (*Micropterus* spp.) species. These changes were associated with reductions in phosphorus concentration and increases in water clarity and summer temperature. Results of a comparative field study conducted on 13 regional lakes indicate significant positive associations between concentrations of total phosphorus and chlorophyll *a* and zooplankton and walleye density. These data suggest that bottom-up effects are limiting walleye abundance either directly or in combination with abiotic conditions that favour bass over walleye.

Résumé : Nous évaluons dans notre étude les changements de la communauté des piscivores dans quatre grands lacs peu profonds de la région des Lacs Kawartha du centre de l'Ontario, Canada, pendant la période de 1980 à 2003 et nous les relions aux variations temporelles de concentration de phosphore, de clarté de l'eau et de température. Sur la période de 24 ans de collecte de données, il y a eu à l'échelle régionale un déclin de l'abondance relative du doré (*Sander vitreus*) et un accroissement de l'abondance relative des espèces d'achigans (*Micropterus* spp.). Ces changements sont reliés à une réduction de la concentration de phosphore et une augmentation de la clarté de l'eau et de la température estivale. Les résultats d'une étude de terrain comparative de 13 lacs de la région montrent une association positive significative entre le phosphore total et la chlorophylle *a*, d'une part, et la densité du zooplancton et celle du doré, d'autre part. Ces données laissent croire que des effets ascendants limitent l'abondance des dorés directement ou alors qu'ils se combinent avec les conditions abiotiques pour favoriser les achigans plutôt que les dorés.

[Traduit par la Rédaction]

Introduction

A topic of great interest to community ecologists is the degree to which abiotic and (or) biotic factors dominate or interact as controlling forces in the regulation of aquatic communities (Pinel-Alloul et al. 1995). There are many factors known to affect the dynamics of warmwater and coolwater fish communities in north temperate lakes, in which walleye (*Sander vitreus*), smallmouth bass (*Micropterus dolomieu*) and largemouth bass (*Micropterus salmoides*) are the dominant piscivores. Nutrient status, light, water clarity, and water temperature are known to be several of the most important abiotic factors (e.g., Downing and Plante 1993; Brazner and Beals 1997; Idrisi et al. 2001).

Changes in the concentrations of available nutrients can influence lake productivity and the composition of aquatic communities. Changes in the productivity of an aquatic ecosystem can alter the habitat (because of changes in the abundance of submerged macrophytes or water clarity) and the availability of food resources. These changes can create conditions favourable to one species or another and result in shifts in fish community composition. The relationship between nutrient levels, primary productivity, and fish production in north temperate lakes has been demonstrated by several authors (Persson et al. 1991; Peltonen et al. 1999; Olin et al. 2002). In a study of 23 fish communities, Downing et al. (1990) found that the production of the entire fish community was highly correlated with phytoplankton pro-

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duction, mean total phosphorus concentration, and annual average fish standing stock.

Light is known to affect the dynamics of fish communities, because changes in light regimes can create conditions favourable to one species or another. Light is considered to be one of the most important determinants of the seasonal and diurnal behavior of walleye, as well as one of the principle factors determining their natural geographic distribution (Ryder and Kerr 1989; Brazner and Beals 1997). Walleye are known to be to be dependent on conditions of low light intensity, as light affects the location and timing of their feeding activity (Ryder and Kerr 1989; Lester et al. 2002, 2004). Given that walleye are highly adapted to specific light regimes, light intensity can potentially be viewed as an ecological constraint that determines the relative dominance of walleye in the community (Ryder and Kerr 1989).

Unlike walleye, the habitat use of *Micropterus* spp. is not restricted by high turbidity; in fact, they are well adapted to feeding in clear water conditions (Ryan et al. 1999; Vanderploeg et al. 2002). Because largemouth and smallmouth bass frequently occur in waterbodies where walleye are also present, changes in water clarity could create conditions preferred by one species but not others at the same trophic level (Brazner and Beals 1997; Casselman et al. 1999; Lester et al. 2004). At the synecological level, changes in water clarity could alter fish community structure by shifting the competitive advantage from one species to another, where at any given time the dominant species would be determined by light conditions (Ryder and Kerr 1989).

Climate change, resulting in a change in water temperature over time, is becoming increasingly recognized as a factor that influences fish and aquatic communities (e.g., Casselman 2002). There is evidence that increased water temperatures have affected the abundance and distribution of fish (Shuter and Post 1990; Casselman et al. 1999), as well as available thermal habitat (Magnuson et al. 1988; Lester et al. 2004) and fish growth, recruitment, and survival (Casselman 2002; Casselman et al. 2002). Changes in temperature can influence the relative abundance of species because the effects of temperature on year-class strength, recruitment, growth, and survival affect each species differently depending on their thermal requirements (Shuter and Post 1990; Tonn 1990; Casselman 2002). In eastern Lake Ontario, it has been predicted that an increase in water temperature of 1 °C above the mean would result in an almost 2.5-fold increase in the relative recruitment of smallmouth bass, whereas coolwater species would experience a 2.4-fold decline in relative recruitment (Casselman 2002). Changes in temperature could also indirectly affect fish communities, for example, by influencing resource partitioning and feeding relations (competition and predation between species) (Tonn 1990). Elevated water temperatures can also alter the species composition of the fish community because of changes in the abundance and species composition of phytoplankton, zooplankton, and benthic macroinvertebrates (Magnuson et al. 1994).

In this study, we examine historical changes in the piscivore community of a group of large, shallow lakes in central Ontario that have experienced historical changes in nutrients, water clarity, and water temperature. Our objectives were to characterize changes in the absolute and relative abundance of piscivore species in these lakes and to assess whether any such changes were related to temporal shifts in nutrient concentration, turbidity, and (or) temperature. We hypothesized that any temporal changes in phosphorus concentration would affect the productivity of the piscivore guild and the relative abundance of walleye in these lakes as a result of shifts in the availability of habitat and food resources. We also hypothesized that any temporal changes in turbidity and (or) temperature would affect the relative abundance of walleye and the two species of bass present in these lakes, given the differences in temperature and turbidity preference between these species. To increase our understanding of the factors affecting piscivore community shifts, we also conducted a comparative field study to examine the relationships between phosphorus concentration, indicators of lower trophic level productivity, and population density of the walleye, a piscivore species believed to be experiencing a major decline in the region. We hypothesized that the availability of phosphorus determines the productivity of these systems, and we predicted that the standing stock of succeeding trophic levels, as well as walleye, would increase with phosphorus concentration.

Materials and methods

Study area

The study was conducted in the Kawartha Lakes, a series of connected waterbodies located in central Ontario that are heavily used for cottaging, recreational and tournament fishing, camping, boating, and canoeing (Fig. 1). There has been extensive shoreline development around the lakes and much of the surrounding watershed has been developed for residential purposes or is used for intensive agriculture. Several exotic species, including the zebra mussel (*Dreissena polymorpha*), bluegill (*Lepomis macrochirus*), black crappie (*Pomoxis nigromaculatus*), and Eurasian watermilfoil (*Myriophyllum spicatum*), have spread into these lakes (Deacon 1992; Mercer et al. 1999). Historically, these lakes have experienced changes in nutrient levels, water quality, and turbidity, which can be attributed to the introduction of exotic species, changes in land-use patterns, and the result of federally mandated programs implemented in the 1970s to reduce phosphorus loading in lakes by limiting phosphates in detergents and reducing flows and concentrations at sewage treatment plants (Stevens and Neilson 1987).

Four of the Kawartha Lakes (Buckhorn, Rice, Scugog, and Balsam) have long-term fish community data. These lakes are highly variable with respect to nutrient status, angling effort, and yield of the piscivore guild (Table 1). The piscivore guild in all of the Kawartha Lakes consists of walleye, largemouth and smallmouth bass, and muskellunge (*Esox masquinongy*) (Deacon 1992). The lakes also contain pumpkinseed (*Lepomis gibbosus*), bluegill, rock bass (*Ambloplites rupestris*), black crappie, yellow perch (*Perca flavescens*), brown bullhead (*Ameiurus nebulosus*), white sucker (*Catostomus commersoni*), and several other cyprinid and percid species.

For the aspect of this study related to present-day fish communities, nine lakes in central and eastern Ontario were added to the aforementioned study lakes (Table 1). Three of these lakes are part of the Kawartha system, and the remain-

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Fig. 1. Location of Kawartha study lakes on the insert map, and the additional lakes in eastern Ontario, Canada.

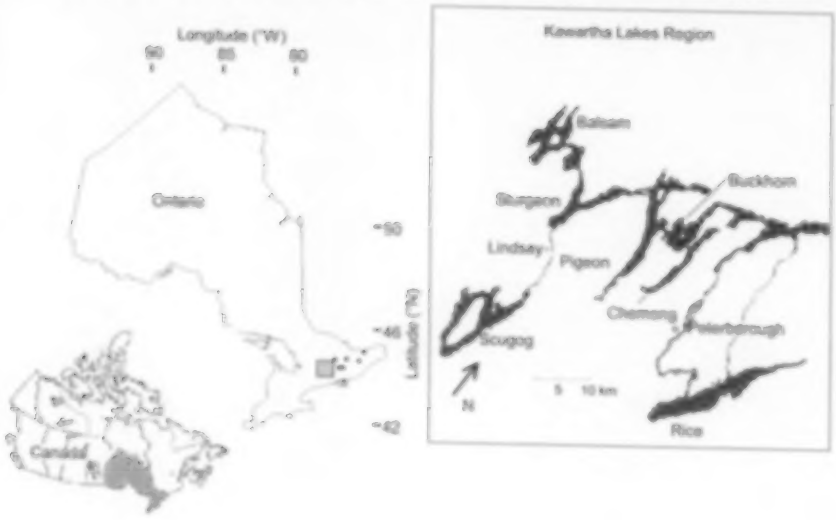

Table 1. Characteristics of the study lakes in the Kawartha and eastern Ontario regions.

Lake	Latitude (N), longitude (W)	Surface area (ha)	Mean depth (m)	Maximum depth (m)	Mean summer Secchi depth (m)	Total phosphorus ($\mu g \cdot L^{-1}$)
Kawartha Lakes						
Balsam	44°35′01″, 78°50′38″	4 665	5.0	14.9	3.6	11.4
Buckhorn	44°29′20″, 78°23′30″	3 191	2.1	9.4	2.3	18.3
Chemong*	44°23′19″, 78°23′35″	2 280	2.4	6.7	2.6	14.3
Pigeon*	44°28′15″, 78°29′42″	5 349	3.0	14.9	2.2	14.7
Rice	44°10′19″, 78°10′35″	10 018	2.3	7.9	1.9	28.8
Scugog	44°08′45″, 78°55′26″	6 347	1.3	7.0	1.1	27.0
Sturgeon*	44°27′58″, 78°42′42″	4 495	2.8	12.2	3.2	16.0
Eastern Ontario lakes						
Christie*	44°48′16″, 76°26′20″	654	8.5	18.3	3.5	10.3
Crotch*	44°54′45″, 76°48′35″	1 677	8.4	32.2	5.5	9.1
Jack*	44°41′38″, 78°01′29″	1 221	8.4	42.7	4.9	14.2
Mississippi*	45°04′01″, 76°09′57″	2 351	2.7	9.2	3.8	14.5
Moira*	44°29′08″, 77°27′07″	822	3.9	11.0	3.0	17.6
Stoco*	44°28′31″, 77°17′20″	503	4.0	9.8	2.1	20.2

Note: Asterisk (*) indicates lakes that were used only for the comparative field study (source: M. Rawson, Kawartha Lakes Fisheries Assessment Unit, Ontario Ministry of Natural Resources, Lindsay, ON K9V 4T7, unpublished data).

ing six are located in eastern Ontario, an area with geology, climate, and land use similar to that of the Kawartha Lakes region. All of the study lakes contain walleye and had been subjected to a fish community survey using multimesh gillnets within a 3-year period.

Assessment of historical changes in the piscivore community and factors affecting community shifts

Spring Index Netting (SIN) trapnet surveys conducted by the Ontario Ministry of Natural Resources (OMNR) were used as a source for historical time series data on the abundance of piscivore species in the four Kawartha study lakes. Trapnet surveys had been conducted in these lakes at 2- to 3-year intervals from 1978 to 2003. In years before 2000, four fixed sites were sampled, whereas in subsequent years, two fixed sites were sampled. Sites were fished for nine consecutive nights. SIN surveys were usually conducted in Rice and Balsam lakes in early to mid-May and in Buckhorn and Scugog lakes in early to mid-June; however, there were a few years when these surveys were conducted in other time periods. To standardize the data for our analysis, we only included surveys conducted from 1 to 15 May in Rice and Balsam lakes when water temperatures were typically between 10 and 15 °C, and 1 to 15 June in Buckhorn and Scugog lakes when water temperatures were typically between 16 and 22 °C. In our analysis, catch rate was expressed as the geometric mean number of fish caught in a 24-h set. The annual mean per lake was calculated by averaging site means because each site was not always sampled an equal number of times.

Data collected from the trapnet surveys were used to address the objectives pertaining to historical changes in the piscivore assemblages and piscivore community structure.

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Pearson correlations were used to assess directional change in catch rates over time. Analyses were conducted for the overall piscivore guild in each lake, as well as individual species for absolute abundance (indicated by catch-per-unit-effort (CPUE)) and relative abundance of walleye, largemouth bass, smallmouth bass, and muskellunge (the mean proportion of that species in trapnet samples). For this analysis, we report individual probability values. Although this does not guarantee that a significant result did not occur by chance, we follow the "logical interpretation" criterion of Moran (2003) and interpret overall patterns in the data rather than any particular correlation.

To assess possible factors resulting in temporal changes to the piscivore community, we analyzed temporal changes in the relationship between relative walleye abundance and total phosphorus concentration, turbidity, and temperature in the four Kawartha study lakes using data from 1980–2003. Total phosphorus concentration and turbidity data were obtained from the Ontario Ministry of Energy and Environment Provincial Water Quality Monitoring Network (PWQMN), a long-term water quality monitoring program. Water samples were collected monthly during the ice-free season from the lake outlets. We used data from Balsam, Buckhorn, Scugog, and Rice lakes collected from 1965 to 2002, averaging phosphorus concentration and turbidity values from samples taken between May and September in the same year to provide an annual mean value for each lake. To assess the long-term relationship between temperature and relative walleye abundance, we used mean monthly summer air temperatures (May to September) for Peterborough, Ontario, from 1980 to 2002, available from the weather station at Trent University.

Assessment of relationships among phosphorus concentration, lower trophic levels, and walleye abundance: comparative field study

The relationship between walleye abundance and the productivity of lower trophic levels, forage fish, and water clarity were examined in a comparative field study that focused on present-day walleye populations for the reasons previously described. The lower trophic levels considered were phytoplankton (as indicated by chlorophyll *a* concentration), zooplankton, and forage fish. Total phosphorus concentration was used as an indicator of lake productivity. Secchi depth was also used in the analysis to examine the relationship between walleye abundance and water clarity.

We used CPUE data from the OMNR Fall Walleye Index Netting (FWIN) program as an indicator of walleye abundance in our study lakes. This gillnetting survey provides an index of walleye abundance, but it is not a suitable community assessment technique because of the large mesh sizes used (25–152 mm) and other biases inherent to gillnetting (species, behaviour, body shape, and size selectivity) (Nielsen and Johnson 1983). Although there are insufficient data to test the relationship between walleye CPUE determined from FWIN and SIN surveys, there is a strong correlation between walleye CPUE assessed with FWIN and that obtained from the Early Summer Trapnetting (ESTN) procedure in the same lake and year ($r = 0.85$, $P < 0.001$, $n = 20$; K. Vascotto, Kawartha Lakes Fisheries Assessment Unit, Ontario Ministry of Natural Resources, Lindsay, ON K9V 4T7, unpublished data). ESTN and SIN are 24-h procedures that employ the same gear, but the former uses random instead of fixed sites.

FWIN surveys were conducted on Balsam and Sturgeon lakes in 2001, Rice Lake in 2003, Lake Scugog in 2002, Pigeon, Buckhorn, and Chemong lakes in 2000, and all other lakes in 2001. The sample gear consists of eight panels 7.6 m long × 1.8 m deep with a total length of 61 m (for further details on survey design see Morgan (2002)). The number of sets per lake was based on lake surface area and morphometry and ranged from 20 to 36 per lake. Total length and weight of each fish were recorded. CPUE was expressed as the geometric mean number of walleye caught per net lift.

The 13 lakes used in the comparative field study were sampled in 2003 for total phosphorus concentration, chlorophyll *a* concentration, and zooplankton density. Three replicate samples were collected per lake, one from a site in each of the major basins. Sampling was conducted monthly from May to October for all parameters except total phosphorus.

Water samples for total phosphorus analysis were collected in mid-May 2003, with three 5-m integrated samples taken from the deepest point in each lake. Samples were run through a 120 µm filter (Dillon and Rigler 1974; Idrisi et al. 2001), transferred to 40 mL acid-washed glass tubes, and stored on ice. Visible spectophotometry was used to assess the total phosphorus concentration in the samples (Ministry of the Environment 1983).

For chlorophyll *a* analysis, water samples were taken by lowering a 1-L amber glass bottle through the photic zone. Secchi depth was taken at the same time and was used to determine the depth of the photic zone, which was defined as 2 × Secchi depth (Dillon and Rigler 1974; Lasenby 1975). When the length of the sample exceeded the depth of the lake, the bottle was lowered to 0.2 m off the bottom. Chlorophyll *a* samples were filtered on Whatman glass microfibre (GF/C), 1.2 µm filters. Filters were fixed with 1 mL of saturated $MgCO_3$ and frozen, and 95% ethanol was used for the extraction of chlorophyll *a*. Chlorophyll *a* concentration was measured by spectophotometry at absorbencies of 665 nm for total chlorophyll, 649 nm for chlorophyll *b*, and 750 nm for turbidity (Lind 1979).

A zooplankton sample was collected using a vertical tow from approximately 1 m off the bottom to the surface of the water with a 72 µm mesh nylon net (mouth diameter, 0.13 m; length, 1.5 m). Zooplankton were preserved in 70% ethanol. Before processing, samples were diluted to 90 mL with ethanol and mixed in a multisided Vertis flask, and three replicate 4 mL subsamples were taken (Fox and Flowers 1990). Subsample counts were averaged to obtain sample density estimates. Individuals were counted using a plankton wheel, and zooplankton density was calculated from vertical tow volumes.

The relative abundance of forage species in each lake was determined from the catches of cyprinids and young-of-year yellow perch, walleye, and centrarchids. Forage fish sampling was conducted with funnel traps (cylindrical wire mesh traps 90 cm long, 40 cm in diameter, 10 cm funnel opening) and standard minnow traps between 29 July and 27 August 2003 in six of the 13 sites (the six Kawartha lakes). Sample sites were selected randomly from all available littoral sites and were distributed throughout the lake. Sites ranged in depth from 1.1 to 4.2 m.

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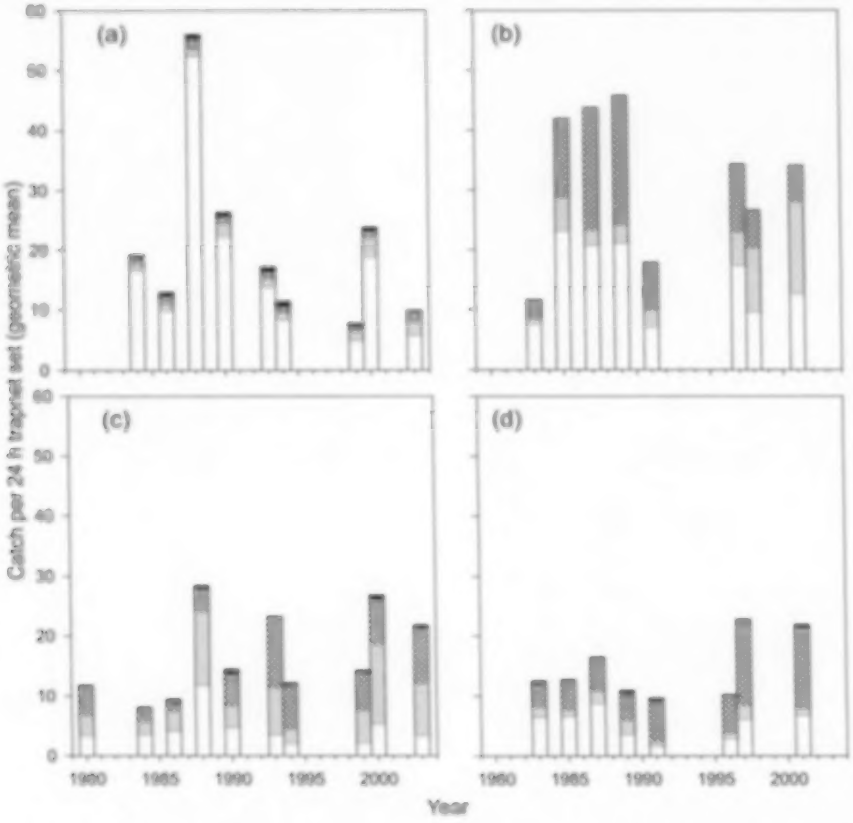
Fig. 2. Temporal changes in catch-per-unit-effort (CPUE) of piscivore species from 1980 to 2003 based on Spring Index Netting trapnet surveys in (*a*) Lake Scugog, (*b*) Rice Lake, (*c*) Balsam Lake, and (*d*) Buckhorn Lake. CPUE is expressed as the geometric mean number of fish caught by species per night per trapnet. Catches: walleye (*Sander vitreus*), open bars; smallmouth bass (*Micropterus dolomieu*), shaded bars; largemouth bass (*Micropterus salmoides*), cross-hatched bars; and muskellunge (*Esox masquinongy*), solid bars.



At each sampling site, one minnow trap and one funnel trap were placed on the substrate, and a second minnow trap was suspended 1 m above the bottom. Traps were baited with dog food, set in the morning, and recovered 24 h later. Fish present in the traps were identified to species and measured for total length. The combination of fish caught in the three traps per site was treated statistically as one trap unit. The number of sites sampled per lake varied from 42 to 61, as a result of inclement weather during sampling days and losses due to tampering or vandalism.

We analyzed the strength of the relationships between walleye CPUE and the productivity of lower trophic levels, forage fish, and water clarity using Pearson correlations. A $\log_{10}(x + 1)$ transformation was used to correct for non-normality of the walleye data.

Results

Historical changes in abundance of the piscivore community and of individual species

CPUE in all four lakes demonstrated a high degree of variability among years (Fig. 2). Piscivore CPUE peaked in three of the four lakes in either 1988 or 1989. Buckhorn Lake, the exception, had a secondary peak in 1987, but the highest overall CPUE did not occur until 1997. A temporal analysis of catch rates provides no indication that there has been an overall decline in the abundance of the piscivore guild, as only one of the lakes showed a negative trend over time and it was not statistically significant (Table 2).

The most consistent change in species abundance over time was the decline in walleye. Walleye CPUE declined in all lakes from 1980 to 2003; however, the declines were not statistically significant (Fig. 2; Table 2). Walleye CPUE exhibited a tendency to peak in all lakes in the late 1980s, followed by a decline in subsequent years. This trend was more pronounced in Lake Scugog than in the other lakes, where the patterns in walleye CPUE were reflected in the decline in total piscivore CPUE from 1989 to 2003.

In contrast to walleye, CPUE of *Micropterus* spp. showed an increasing trend in all lakes from 1980 to 2003. Three of the four lakes exhibited an increase in smallmouth bass CPUE, although this increase was only significant in Rice Lake (Table 2). However, the fourth lake, Buckhorn, exhibited a significant increase in largemouth bass CPUE. The increase in

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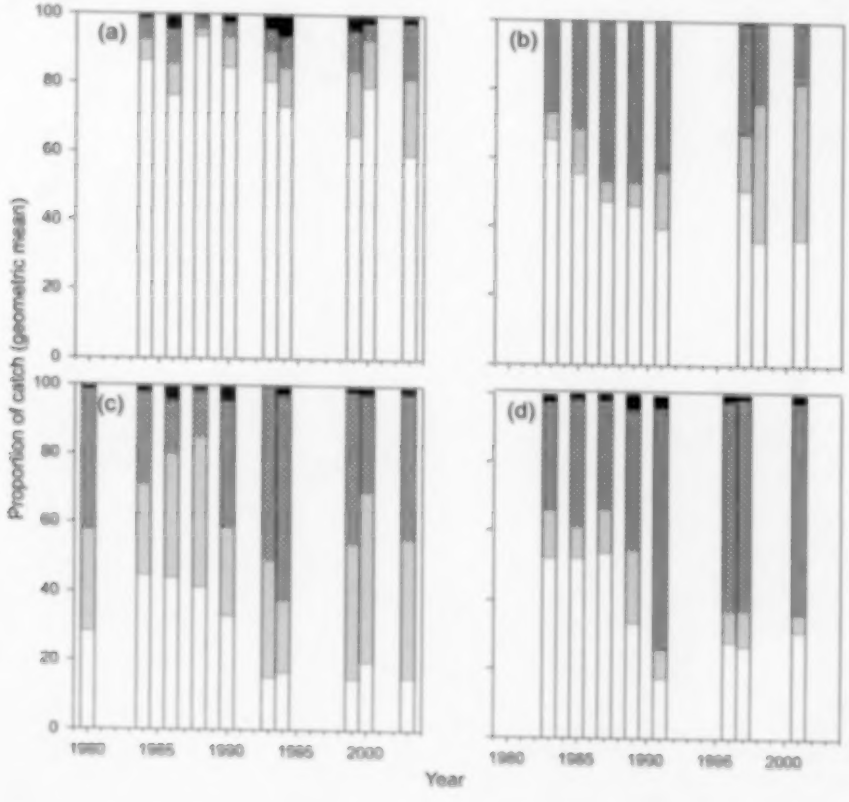
Table 2. Analysis of changes over time in the catches of walleye (*Sander vitreus*), smallmouth bass (SMB; *Micropterus dolomieu*), largemouth bass (LMB; *M. salmoides*), muskellunge (*Esox masquinongy*), and all piscivore species combined.

		Lake Scugog		Rice Lake		Balsam Lake		Buckhorn Lake	
		r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
CPUE	Piscivore guild	–0.38	0.31	0.05	0.92	0.50	0.14	0.56	0.15
	Walleye	–0.41	0.27	–0.24	0.56	–0.19	0.60	–0.20	0.64
	SMB	0.61	0.08	0.84	<0.01	0.50	0.14	–0.16	0.70
	LMB	–0.11	0.79	–0.29	0.49	0.66	0.040	0.85	<0.01
	Muskellunge	–0.26	0.50	–0.01	0.95	0.32	0.36	0.16	0.70
Relative abundance	Walleye	–0.75	0.02	–0.77	0.03	–0.75	0.01	–0.71	0.049
	MB	0.87	<0.01	0.85	<0.01	0.48	0.16	–0.50	0.20
	LMB	0.57	0.13	–0.48	0.24	0.36	0.31	0.80	0.02
	Muskellunge	0.15	0.69	–0.17	0.70	–0.10	0.79	–0.18	0.66

Note: Results are based on Spring Index Netting trapnet surveys conducted from 1980 to 2003 in the four study lakes. Pearson's correlation coefficients (*r*) and individual probability values are shown. Number of data years for each lake is as follows: Balsam ($n = 10$), Scugog ($n = 9$), Buckhorn and Rice ($n = 8$). CPUE, catch-per-unit-effort.

Fig. 3. Temporal changes in the relative abundance of piscivore species from 1980–2003 based on the species composition of trapnet samples in (*a*) Lake Scugog, (*b*) Rice Lake, (*c*) Balsam Lake, and (*d*) Buckhorn Lake. Catches: walleye (*Sander vitreus*), open bars; smallmouth bass (*Micropterus dolomieu*), shaded bars; largemouth bass (*Micropterus salmoides*), cross-hatched bars; and muskellunge (*Esox masquinongy*), solid bars.



largemouth bass CPUE was also significant in Balsam Lake from 1980 to 2003.

An examination of the long-term changes in the relative abundance of piscivores more strongly emphasized the trends in absolute CPUE. Trapnet catches were dominated by walleye until the late 1980s, at which time there was a gradual shift in the species composition of the piscivore guild to favour *Micropterus* spp. (Fig. 3). The decline in the relative abundance of walleye from 1980 to 2003 was significant in all lakes, and three of the four study lakes exhibited

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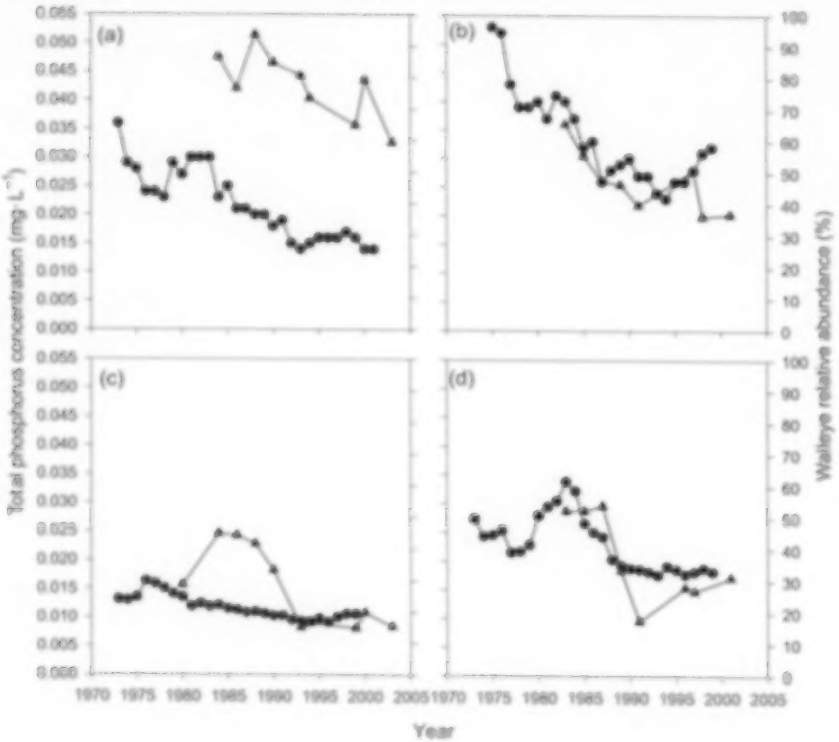
Fig. 4. Comparison of temporal changes in mean summer (May–September) total phosphorus concentration (●) and walleye (*Sander vitreus*) relative abundance (▲) in (*a*) Lake Scugog, (*b*) Rice Lake, (*c*) Balsam Lake, and (*d*) Buckhorn Lake, 1973–2001. The relative abundance of walleye is based on the species composition of Spring Index Netting trapnet samples. Concentration values presented represent 5-year running averages to smooth the variation among years.



a significant increase in relative abundance of either smallmouth or largemouth bass (Table 2).

Environmental factors associated with historical changes in walleye relative abundance

There has been a significant decline in total phosphorus concentration in all four study lakes over the study period ($-0.89 < r < -0.84$, $P < 0.001$; Fig. 4). As previously noted, there were no changes over time in piscivore CPUE, and thus, the relationship between total phosphorus concentration and piscivore CPUE was not significant in any of the lakes. However, the decline in phosphorus over time was accompanied by a decline in the relative abundance of walleye, but the association between the two variables was only significant in Buckhorn Lake ($r = 0.83$, $P = 0.011$). An inspection of individual lake plots suggested that there might be a lag period of several years between the decline in total phosphorus and the decline in relative walleye abundance in the other three lakes. Post-hoc analysis using relative walleye abundance in years subsequent to phosphorus concentration measurement demonstrated the strongest relationships between these variables with an 8-year lag in Balsam Lake ($r = 0.77$, $P = 0.016$), a 6-year lag in Rice Lake ($r = 0.75$, $P = 0.031$), and a 7-year lag in Lake Scugog ($r = 0.80$, $P = 0.033$). The decline in phosphorus over time was accompanied by an increase in the relative abundance of *Micropterus* species, but the association between the two variables was only significant in Buckhorn Lake ($r = -0.82$, $P = 0.013$).

Turbidity also exhibited a significant decrease over time in the study lakes ($-0.83 < r < -0.68$, $P < 0.001$ in all cases), with most of this decrease occurring since the late 1980s. As was the case with phosphorus, the relationship between turbidity and piscivore CPUE was not significant in any of the lakes. Years of lower turbidity also tended to be years with a lower relative abundance of walleye (Fig. 5); however, the association between the two variables was only significant in Balsam and Scugog lakes ($r = 0.90$, $P = 0.002$, and $r = 0.82$, $P = 0.013$, respectively). The decline in turbidity over time was accompanied by an increase in the relative abundance of *Micropterus* spp., but the association between the two variables was again only significant in Balsam and Scugog lakes ($r = -0.89$, $P = 0.003$, and $r = -0.82$, $P = 0.014$, respectively).

Average annual summer air temperatures in the region showed a significant warming trend over the period of the historical study ($r = 0.71$, $P < 0.001$). Although the relationship between average annual summer air temperature and piscivore CPUE was not significant, the relationship between mean temperature and the relative abundance of both walleye and *Micropterus* spp. was significant in three of the four

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Fig. 5. Comparison of temporal changes in summer turbidity (●) and walleye (*Sander vitreus*) relative abundance (▲) in (*a*) Lake Scugog, (*b*) Rice Lake, (*c*) Balsam Lake, and (*d*) Buckhorn Lake, 1973–2001. FTU, formazin turbidity units.

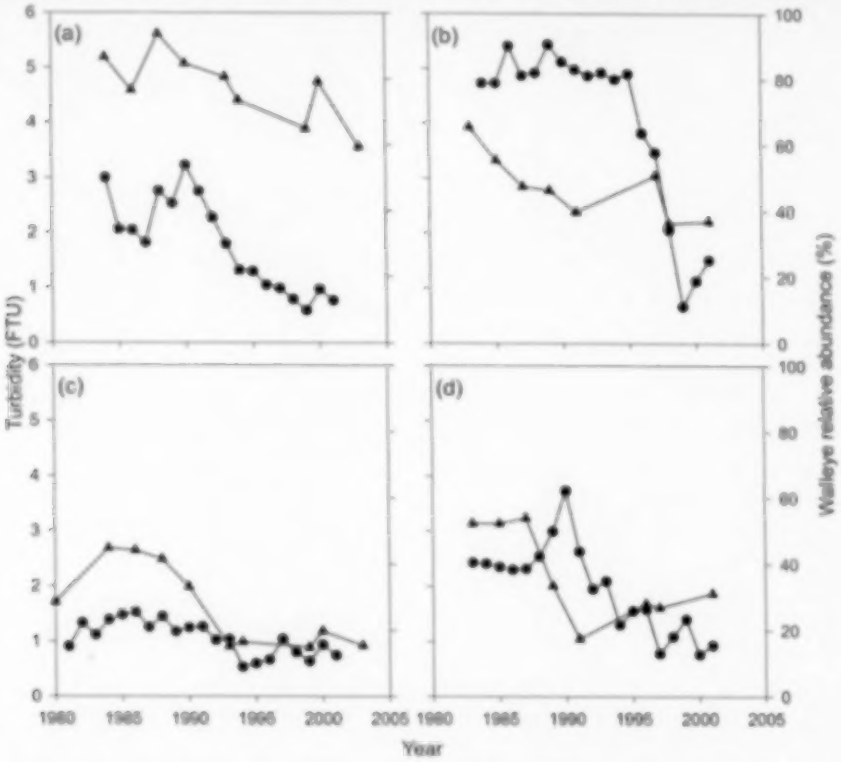

Table 3. Correlations between average annual summer air temperature and piscivore catch-per-unit-effort (CPUE), relative abundance of walleye (*Sander vitreus*), and relative abundance of *Micropterus* species (largemouth bass (*Micropterus salmoides*) and smallmouth bass (*M. dolomieu*) combined), based on Spring Index Netting trapnet surveys conducted from 1980 to 2003.

	Lake Scugog		Rice Lake		Balsam Lake		Buckhorn Lake	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Piscivore CPUE	–0.35	0.36	–0.35	0.39	0.25	0.49	0.22	0.61
Relative abundance of walleye	–0.72	0.03	–0.80	0.02	–0.76	0.01	–0.63	0.09
Relative abundance of *Micropterus* spp.	0.68	0.043	0.80	0.02	0.75	0.01	0.64	0.09

Note: Pearson's correlation coefficients (*r*) and individual probability values are shown. Number of data years for each lake is provided in Table 2.

lakes (Table 3). In all cases, the relative abundance of walleye decreased with increasing temperature, whereas the relative abundance of *Micropterus* increased.

Comparative field study: relationships between phosphorus concentration, lower trophic levels, and walleye abundance

Total phosphorus concentration, chlorophyll *a* concentration, and zooplankton density showed moderate to strong positive correlations across the 13 Kawartha and eastern Ontario lakes, and all three of these factors were negatively correlated with Secchi depth (Table 4). Although all of these factors showed correlations with forage fish CPUE in the expected direction across the six lakes in which forage fish data were collected, none of these relationships was significant.

There were strong positive relationships between contemporary walleye CPUE (based on the FWIN surveys) and total phosphorus concentration, chlorophyll *a* concentration, and zooplankton density, but once again, the correlation between walleye and forage fish CPUE was not significant. There was also a significant negative relationship between walleye CPUE and Secchi depth.

Discussion

The piscivore guild: a history of change (1980–2003)

Over the past 25 years, fish communities in the Kawartha Lakes have experienced dramatic changes in species composition and relative abundance. A decline in turbidity due to the reduction in nutrient loading and the invasion of zebra

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Table 4. Correlation matrix for trophic interactions: total phosphorus concentration, chlorophyll *a* concentration, zooplankton density, forage fish catch-per-unit-effort (CPUE), and walleye (*Sander vitreus*) CPUE (Fall Walleye Index Netting surveys) in 13 lakes in the Kawartha and eastern Ontario regions (six lakes for forage fish).

	Total phosphorus		Chlorophyll *a*		Zooplankton		Forage fish		Walleye	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Total phosphorus	—	—	—	—	—	—	—	—	—	—
Chlorophyll *a*	0.89	<0.001	—	—	—	—	—	—	—	—
Zooplankton	0.58	0.040	0.76	<0.001	—	—	—	—	—	—
Forage fish	0.47	0.34	0.63	0.19	0.22	0.68	—	—	—	—
Walleye	0.63	0.02	0.77	<0.001	0.79	<0.001	0.55	0.26	—	—
Secchi depth	–0.86	<0.001	–0.90	<0.001	–0.68	0.01	–0.34	0.51	–0.66	0.01

Note: Analysis was based on $\log_{10}$-transformed means for each lake. Pearson's correlation coefficients (*r*) and individual probability values are shown. See text for dates and methods of data collection.

Table 5. Coefficients of variation for the catch-per-unit-effort (CPUE, %) and relative abundance (RA, %) of walleye (*Sander vitreus*), smallmouth bass (*Micropterus dolomieu*), largemouth bass (*Micropterus salmoides*), and muskellunge (*Esox masquinongy*).

	Lake Scugog		Rice Lake		Balsam Lake		Buckhorn Lake	
Species	CPUE	RA	CPUE	RA	CPUE	RA	CPUE	RA
Walleye	86	14	44	21	63	46	45	38
Smallmouth bass	42	56	83	80	64	26	41	43
Largemouth bass	23	52	61	33	53	42	55	32
Muskellunge	39	57	127	119	59	60	39	53

Note: Results are based on Spring Index Netting trapnet surveys conducted from 1980 to 2003 in the four study lakes.

mussels are factors likely to have contributed to changes in the fish communities in these lakes. Over the period from 1980 to 2003, there has been a significant change in the composition of the piscivore communities, with a significant decrease in the abundance of walleye relative to that of the two *Micropterus* species. During that period, there were no significant temporal changes in the overall abundance of piscivores and few significant changes in the abundance of any piscivore species in any of the lakes.

The general absence of significant changes through time in the CPUE of individual piscivore species may be the result of low power to detect these changes as a result of high interannual variability in the abundance of these species. In contrast, the proportions of the species are less subject to fluctuation than the absolute abundance of individual species, probably because some environmental variables that vary from one year to the next affect all species similarly. The lower variability in species proportions is illustrated by the coefficients of variation, which in the majority of cases were lower for relative abundance of a species than for CPUE (Table 5). These results suggest that there could be overall changes in the absolute abundance of these species consistent with the changes in relative abundance that we are unable to detect with our present time series.

Over the past three decades, the Kawartha Lakes have been undergoing the process of oligotrophication, as well as a significant decline in turbidity. Cultural oligotrophication resulting from a federally legislated reduction in the phosphate content of detergents was the likely reason for the initial decline in total phosphorus concentrations in the 1970s. The invasion and establishment of filter-feeding zebra mussels in the Kawartha Lakes beginning in 1994 (Mercer et al. 1999) has also contributed to the processes of biological oligotrophication and increased transparency. The decline in total phosphorus concentrations over the past 25 years may not have a detectable influence on the overall productivity of the piscivore guild. Nevertheless, phosphorus reductions may have affected other aspects of the aquatic ecosystem in such a way as to create conditions that favour one species over another. One such parameter that would likely be affected by lowered phosphorus concentrations is water clarity.

Trophic interactions and lake productivity

In a contemporary context, there were strong correlations between total phosphorus concentration, Secchi depth, chlorophyll *a* concentration, and zooplankton density in the 13 study lakes. There were also strong positive relationships between walleye CPUE in gillnets and the productivity and trophic indicators for these lakes, as well as a negative relationship between walleye CPUE and Secchi depth. Although there were no significant relationships between forage fish CPUE and any of the other variables, this may have been due to the small number of lakes available to test this association (6 vs. 13 for the other variables tested) or because of gear biases associated with the use of minnow and funnel traps.

It has long been established that nutrients (and especially phosphorus) are a major factor determining the primary productivity of aquatic ecosystems in north temperate regions (Downing et al. 1990; Matveev 1995; Olin et al. 2002). A decline in nutrient availability has been related to a decline in primary productivity, as well as to an increase in water clarity (Dillon and Rigler 1974; Mazumder et al. 1988; Prairie et al. 1989). As previously noted, the decline in total

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phosphorus concentrations in the Kawartha Lakes appears not to have had a significant influence on the productivity of the piscivore guild, but it seems to have altered the aquatic ecosystem in such a way as to create conditions that favour bass over walleye. In accordance with the bottom-up theory, the decline in nutrients should result in reduced food abundance and a corresponding decline in overall piscivore biomass. Although such a decline is not yet evident, we would expect it in the future if nutrient concentrations continue to decline, and ultimately, *Micropterus* should also be affected.

Temporal changes in the piscivore guild and water clarity

There has been a significant decline in turbidity in all four Kawartha Lakes from a high in 1988–1990. Our hypothesis that any temporal changes in turbidity would affect the relative abundance of walleye was supported by the general decline in the relative abundance of walleye in trapnets since the late 1980s and the corresponding decline in turbidity during the same period. There was a significant relationship between contemporary Secchi depth and walleye CPUE in gillnet surveys, which when combined with the historical data, suggests that changes in the past may have influenced the abundance of walleye.

It has been shown that increased water clarity can alter the species composition of fish communities by reducing the competitive advantage that walleye have over *Micropterus* spp. to thrive in conditions with low water clarity (Ryder and Kerr 1989; Casselman et al. 1999). Under conditions of increased water clarity, the reduced ability of walleye to detect and capture prey would have resulted in a decline in its foraging success. *Micropterus* spp. are not restricted in the same manner by water clarity and are actually better adapted to feeding in conditions of increased water clarity and abundant macrophytes (Ryan et al. 1999; Vanderploeg et al. 2002). The observed decline in turbidity may therefore have increased prey consumption rates of *Micropterus* spp. despite a possible decline in abundance of some prey.

Similarly dramatic ecosystem level changes have occurred in Lakes Ontario, Erie, and St. Clair since the 1970s, changes that have resulted in major ecological effects on the Great Lakes ecosystems and the fish community dynamics in these lakes (Casselman et al. 1999; Ryan et al. 1999; Mills et al. 2003). Lakes Ontario and Erie have experienced a major increase in water clarity because of a reduction in nutrient loading, beginning in the 1970s and later with the establishment of zebra mussels in the early 1990s (Mills et al. 1993; Casselman et al. 1999). In the lower Bay of Quinte, Lake Ontario, walleye abundance declined in the early 1990s (Mills et al. 2003); the decline was attributed to changes in the distribution of walleye. This stock dispersed from the lower Bay of Quinte into the eastern basin of Lake Ontario following a progressive increase in water clarity attributed to the zebra mussel introduction (Casselman et al. 1999; Mills et al. 2003). An empirical model developed by Chu et al. (2004) indicated that the lack of suitable light limits the walleye habitat in the Bay of Quinte and that recent declines in walleye stocks could in part be attributed to a decline in available habitat (primarily as a result of light and temperature changes). In Lake St. Clair, an increase in water clarity as a result of zebra mussel filtration and an increase in submerged macrophyte abundance has had major consequences for piscivore species (Vanderploeg et al. 2002). There was a fivefold increase in macrophyte abundance, which increased the amount of spawning and feeding habitat for muskellunge, smallmouth bass, and yellow perch but decreased the quality and quantity of the habitat preferred by walleye. Vanderploeg et al. (2002) attributed a threefold increase in smallmouth bass and muskellunge abundance and a 50%–75% decline in walleye abundance between 1986 and 1994 to the increased water clarity and changes in habitat. A habitat supply model developed by Lester et al. (2004) to predict the availability of walleye habitat based on water clarity, temperature, and bathymetry was applied to Lake St. Clair. They predicted that the increase in water clarity in the lake resulting from the invasion of zebra mussels would result in a greater than 50% loss of walleye habitat, which supported independent assessments showing that walleye abundance had declined proportionately (Lester et al. 2004).

These studies from the Great Lakes region suggest that changes in water clarity would be expected to influence fish community structure because of the effect of increased transparency on the suitability of walleye habitat. As a result of the introduction of zebra mussels, decreased phosphorus loading, and reduced turbidity, the Kawartha Lakes have changed towards a clear-water macrophyte-dominated system that provides feeding and spawning habitat for smallmouth and largemouth bass, yellow perch, and muskellunge, while habitat for walleye has been lost. Therefore, as Ryder and Kerr (1989) suggested, light may indeed act as a constraint on the system that determines the relative abundance of walleye. However, water clarity is only one of several factors acting in concert that influences the structure of fish communities of the Kawartha Lakes.

Changes in turbidity and the productivity of lower trophic levels may explain the shifts in species composition in these lakes because they differentially affect species based on their habitat preferences and feeding strategies. Changes in temperature can influence the species composition in lakes because of its effects on year-class strength, recruitment, growth, and survival (Shuter and Post 1990; Casselman 2002). The increased temperatures of the past decade observed in the Kawartha Lakes region coincided with an increase in the CPUE and relative abundance of *Micropterus* spp. and a decline in walleye during this same period. In the Kawartha Lakes region, walleye are at the southern extent of their distributional range, whereas smallmouth bass are in the more northerly portion of their range (Scott and Crossman 1973). As a result, the effects of increased temperatures may be more pronounced in this region because these species are at the edge of their distributional ranges and are therefore more sensitive to changes in environmental conditions (Scott and Crossman 1973; Shuter and Post 1990; Casselman et al. 2002).

Temperature has had a major influence on species abundances and community dynamics in eastern Lake Ontario and the Bay of Quinte (Casselman et al. 1999; Mills et al. 2003). Increased water temperatures appear to have had a positive effect on warmwater fish species, including smallmouth and largemouth bass. In recent years, the strongest year classes of smallmouth bass have been associated with the above average temperatures of the El Niño years (1983, 1987–1988, and 1995), which resulted in increased summer

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water temperatures (Casselman et al. 2002). Casselman et al. (2002) reported a highly significant positive correlation between year-class strength of smallmouth bass and July–August water temperatures over the period from 1976 to 1996.

In the Kawartha Lakes, as in eastern Lake Ontario, future increases in summer temperatures could significantly affect year-class strength and result in changes in fish community structure. For example, an increase in water temperature could substantially increase the relative recruitment of *Micropterus* spp. and decrease the relative recruitment of walleye (and other coolwater species), which has the potential to alter fish community dynamics (Casselman 2002; Casselman et al. 2002).

An alternate explanation to the changes over time in the Kawartha Lakes fish communities is that high angling effort and yield of walleye relative to *Micropterus* spp. was tilting the balance against the former and in favour of the latter. Although creel survey data from 1980 to 2003 (M. Rawson, Kawartha Lakes Fisheries Assessment Unit, Ontario Ministry of Natural Resources, Lindsay, ON K9V 4T7, unpublished data) do suggest that walleye yields were higher than largemouth or smallmouth bass yields until the mid-1990s, the relative abundance of walleye continues to decline despite the drop in fishing effort and yield of walleye and an increase in bass yield since that period. Furthermore, the creel data indicate that walleye yield has declined in three of four study lakes over the period from 1980 to 2003 and since 1993 in Lake Scugog (M. Rawson, Kawartha Lakes Fisheries Assessment Unit, Ontario Ministry of Natural Resources, Lindsay, ON K9V 4T7, unpublished data), with no corresponding increase in walleye abundance. These data do not rule out the likelihood that fishing has had some influence on the balance of piscivores in the Kawartha Lakes, but the overall changes through time in the piscivore community are more consistent with those of phosphorus, turbidity, and temperature than those of fishing yields.

In summary, there have been major changes in the species composition of the piscivore guild in the Kawartha Lakes over the past quarter century. Changes in the piscivore guild in all four lakes appear to be associated with the introduction of exotic species, reduced nutrient loading, shifts in summer temperatures, and possibly other anthropogenic stressors, such as angler overexploitation and increased shoreline modification on the Kawartha Lakes. A decline in turbidity and phosphorus concentration and an increase in summer temperature were factors that corresponded with a decline in walleye relative abundance and an increase in the relative abundance of *Micropterus* spp. in these lakes. Recent data from Kawartha and eastern Ontario lakes show that walleye abundance is strongly correlated with the productivity of lower trophic levels, nutrients, and water clarity.

Overall, the observed changes in the Kawartha Lakes ecosystems and fish communities were not the result of planned, science-based management strategies or experimental research. However, they were the result of a combination of many unintentional and unanticipated biological and anthropogenic stressors. Although many of the changes are probably irreversible, the lessons learned from the past 25 years will provide fisheries managers and scientists with a better understanding of these valuable aquatic ecosystems.

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Comparison and utility of different size-based metrics of fish communities for detecting fishery impacts[1]

Daniel E. Duplisea and Martin Castonguay

Abstract: The use of fish community indicators based on size spectra has become popular in the development of an ecosystem approach to fisheries. Size spectrum theory arose from basic ecological work on energy flow, predator–prey interactions, and biomass standing stock and was later applied to fish communities as length–frequency analysis. A multitude of size spectrum indicators have resulted, but it is not clear if they all present similar information. Here we develop a simple framework describing what four size spectra indicators suggest about fish communities, their likely response to fisheries exploitation, their ecological interpretation, and some of their biases. We examined indicators for scientific survey data from six exploited North Atlantic fish communities for the information that they reveal about each community. Each indicator revealed different information and had different biases. Combining indicators for the most impacted system (owing to fisheries and environmental change), the eastern Scotian Shelf, revealed a pattern analogous to Holling's ecological cycle of exploitation, conservation, release, and reorganisation. If this analogy is generally valid, then it suggests that collapsed fish communities are more susceptible to chance events, and recovery is not directly reversible and may not be recoverable (to previous known state) at all if the system moves to an alternative cycle.

Résumé : Les indicateurs des communautés de poissons basés sur les spectres de taille servent souvent à donner une approche écosystémique aux études halieutiques. La théorie des spectres de taille s'est développée à partir d'études écologiques fondamentales sur les flux d'énergie, les interactions prédateurs–proies et la biomasse des stocks et elle a été appliquée subséquemment aux communautés de poissons sous la forme d'analyses de fréquence des longueurs. Un grand nombre d'indicateurs du spectre de taille ont été proposés, mais il n'est pas clair qu'ils présentent des informations équivalentes. Nous mettons au point un cadre de travail simple pour décrire ce que quatre indicateurs du spectre de taille révèlent au sujet des communautés de poissons et leur réaction probable à l'exploitation par la pêche; nous présentons aussi l'interprétation écologique et certaines des déformations de ces indicateurs. Nous avons évalué les indicateurs à l'aide de données d'inventaire provenant de six peuplements exploités de poissons de l'Atlantique Nord et déterminé l'information qu'ils dévoilent sur chacun des peuplements. Chaque indicateur révèle des informations différentes et présente des déformations particulières. La combinaison des indicateurs pour le système le plus affecté (par les pêches et le changement climatique), soit l'est de la plate-forme néo-écossaise, présente un patron analogue au cycle écologique de Holling, d'exploitation, de conservation, de libération et de réorganisation. Si cette analogie est en gros valide, elle indique que les peuplements effondrés de poissons sont plus vulnérables aux événements aléatoires, que la récupération n'est pas directement réversible et qu'il peut ne pas y avoir de récupération du tout (retour à l'état observé antérieurement) si le système entreprend un cycle de rechange.

[Traduit par la Rédaction]

Introduction

It is now widely acknowledged that an ecosystem approach will be increasingly used for management of exploitation of aquatic systems (World Wildlife Fund (WWF) 2002), though there is not yet a consensus of what an ecosystem approach to fisheries management will entail (e.g., Browman and Stergiou 2004). Clearly, to be useful and acceptable, an ecosystem approach to management will meld socio-economic and ecological considerations (Fisheries Research Conservation Council 1998; WWF 2002), fully acknowledging that this is difficult to achieve (Degnbol 2002). Socio-economic considerations involve consultation among stakeholders to reach consensus on individual actions,

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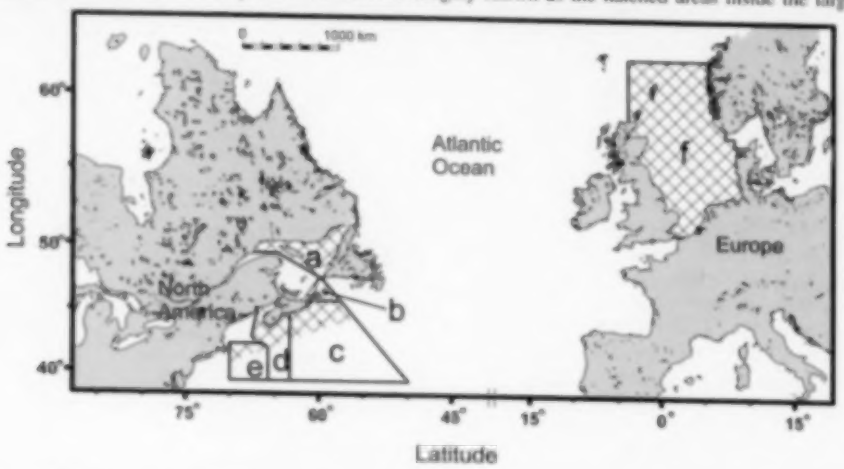
Fig. 1. Map of the different systems studied with statistical management areas demarcated: (*a*) 4RS, northern Gulf of St. Lawrence; (*b*) 4Vn, Sydney Bight; (*c*) 4VsW, eastern Scotian Shelf; (*d*) 4X, western Scotian Shelf; (*e*) 5Z, Georges Bank; (*f*) IVabc, North Sea. Surveys represent continental shelf and shelf slope areas, which are roughly shown as the hatched areas inside the larger statistical areas.



whereas ecological considerations consist of various metrics describing fish stocks, ecosystems, or the environment (e.g., Rice 2000) brought to the table by stakeholders. Science, in this respect, services stakeholders and policy makers to provide useful metrics of the natural system and potential impacts of various actions. Science, therefore, must propose various metrics of the natural system that reflect an amalgam of community characteristics and how a metric responds to perturbations such as commercial fishing.

Size spectra are a common type of metric used in aquatic ecosystems to assess the state of a community (Kerr and Dickie 2001). Size spectra are multispecies indicators of the abundance or biomass of organisms plotted as a function of their body size. Size spectra data are usually statistically fitted with a regression, the parameters of which are used to characterise the system under scrutiny. Size spectra have been used in fisheries to show that exploitation steepens a straight line slope over time (Pope et al. 1988; Bianchi et al. 2000), which indicates a systemic decrease in the abundance of large fish that are preferentially taken by fisheries. Other work corroborates this by showing that fisheries have progressively lowered the trophic level of catches (Pauly et al. 1998), which in aquatic ecosystems corresponds with smaller body size (Jennings et al. 2002). Size spectra are also known to reflect large changes in management imposed on shelf fisheries (Pope et al. 1988; Duplisea and Kerr 1995).

Though size spectra clearly indicate trends in exploited fish communities, several confusing aspects of size spectra exist, with most confusion arising out of methodological and statistical treatment of data, as well as the applicability of certain theory. We believe that the multitude of treatments of size spectra in fisheries, though presently confusing, increases the utility of the approach to provide metrics of fish community state, which could be used in an ecosystem approach to managing fisheries. It is our purpose here to outline some common treatments of size spectra data, what they represent ecologically, how they are likely to respond to fishing, and their inherent biases. We analysed size spectra data from six different systems: the northern Gulf of St. Lawrence, the Sydney Bight, the eastern Scotian Shelf, the western Scotian Shelf, Georges Bank, and the North Sea.

Origins and some common analyses of size spectra

The roots of size spectra can be found in Elton's trophic pyramid (Elton 1927), where abundant, low trophic level, and small body size organisms form the base of the pyramid and the apex contains the rare, large-bodied top predators: conceptually, size spectra are merely Eltonian trophic pyramids turned on their sides. Sheldon's work on plankton in the 1970s examined abundance or biomass in $\log_2$ body size bins and found regularities in vastly different oceanic areas (Sheldon et al. 1972), leading them to propose that the same relative biomass proportion in adjacent body size bins extends from bacteria to whales. Further work showed that the slope of biomass vs. log body weight was negative (Platt and Denman 1978). When fisheries scientists began examining multispecies size distributions, they used length–frequency based analyses (Pope and Knights 1982), usually fitting straight lines to them. Almost invariably, fitted straight line slopes to fish community length–frequency data are negative (Bianchi et al. 2000). Biomass size spectra (log biomass vs. log body weight bins) (Thiebaux and Dickie 1993) have been fitted with quadratics quite well, and a theory underpins such fittings (Dickie et al. 1987).

Size spectra can be constructed using any measurement of organism size combined with a measure of the prevalence of that body size in the system. Additionally, a variety of models can be fitted to size spectra, e.g., straight lines (Pope et al. 1988) and parabolas, to characterise the pattern. No one method is universally correct, and the choice will dependent somewhat on the discipline and the questions being asked of the size spectrum metric.

Given the multitude of methods for size spectra construction and different kinds of statistical model fits that exist in the literature, size spectra work can be confusing, though some work has been done to relate and clarify the methods

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(Han and Straskraba 1998). No single method is correct and we propose that analysing the same data set in several ways can reveal complementary information about the system being studied. It is important to realise which analyses might be useful for particular questions or under which conditions related to data bias.

Materials and methods

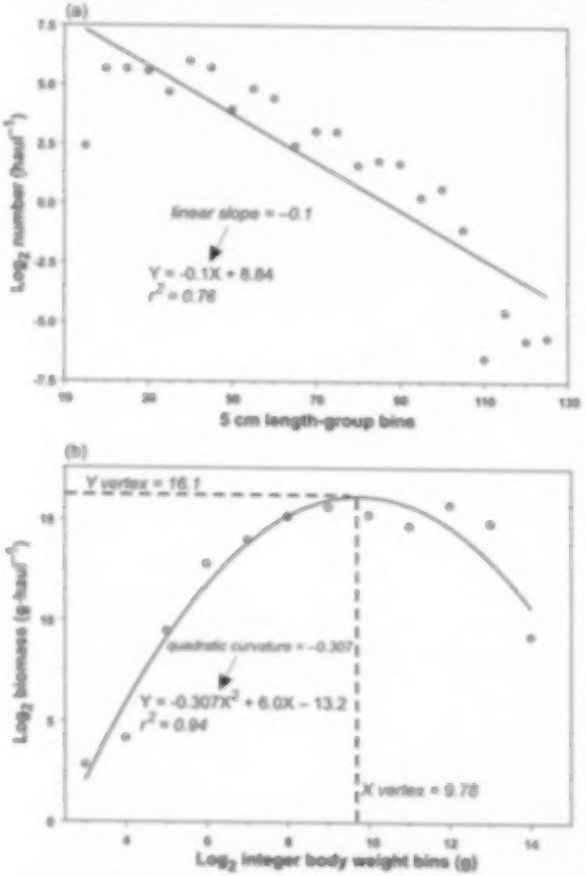
Six different regions (Fig. 1) were studied by examining data from four separate sources: (1) Atlantic Canadian groundfish summer survey for the Scotian Shelf, (2) the Canadian winter trawl survey on Georges Bank, (3) northern Gulf of St. Lawrence groundfish and shrimp summer survey, and (4) the English groundfish summer survey for the North Sea. From survey 1, we obtained data for the Sydney Bight (4Vn) and the eastern (4VsW) and western (4X) Scotian Shelf. From survey 2, we obtained data for Georges Bank (5Z), and from surveys 3 and 4, we obtained data for the northern Gulf of St. Lawrence (4RS) and the North Sea (IVabc), respectively. Each of these survey types has different protocols for fishing and gear and different modes of data storage; hence they were treated separately and are not directly comparable in all respects. The Canadian surveys are represented here under the statistical areas of the Northwest Atlantic Fisheries Organization (NAFO; www.nafo.ca). The English survey is represented under the statistical areas of the International Council for the Exploration of the Sea (ICES; www.ices.dk).

The Canadian surveys utilise a stratified random sampling design (Doubleday 1981) with a standard tow using a benthic otter trawl. For each tow, all the fish were weighed and a subsample (200 individuals per species) was taken for computing length–frequency distributions. These length–frequency distributions were the basis of the data used here. Weights of individuals were used directly if available or were calculated from species-specific length–weight regressions.

The English groundfish survey of the North Sea is conducted by performing standard tows of 0.5 to 1 h duration at fixed stations each year. Tow time and gear changes occurred in the early 1990s. All data were standardised to a 1-h tow.

Our analyses include vertebrates and *Loligo* and *Illex* squids. The vertebrates consisted mostly of teleosts, but a large elasmobranch component is also represented in all the systems. Squids usually constituted only a small portion of biomass in any tow. A complete listing of species included in analyses of each system is available (Supplementary data).[1] This list represents the total potential species pool as not all species were caught in all tows or even in all years. Only seven species had a consistent length–frequency record each year of the northern Gulf survey, but we used all species if they were measured, even though the protocol changed over the survey. We compared analyses (not presented here) conducted on all measured species vs. only the seven core species: the core species usually constituted 80% of the total biomass and changes in the trend in the size spectrum slope did not vary considerably, both showing a shallowing slope from 1990. The all-species slope steepened slightly after 1996, whereas the core-species slope continued shallowing. Because of the noise in the northern Gulf survey and our inability to characterise trends in this system (with all species or just core species), we did not pursue this comparative analysis further.

Fig. 2. Demonstration plots of (*a*) a straight line slope fitted to log number vs. length size spectra and (*b*) a quadratic curve fitted to log biomass vs. log body weight size spectra. Least square fitted size spectra parameters (linear slope, quadratic curvature, *X* vertex, *Y* vertex, and r^2) analysed in this study are shown on the plots. Data shown are for Georges Bank survey data from 1987.



For each system, we constructed two types of multispecies body size abundance distributions, and four size spectrum indicators were derived from these fits: from a length–frequency distribution, where 5 cm body length categories were used and abundance (number·haul^{-1}) within each 5 cm length bin was summed and logged ($\log_2$), the size spectrum metric of a straight line slope was taken from this fitting (Fig. 2*a*). From $\log_2$ biomass (g·haul^{-1}) at $\log_2$ body weight (g) distributions, commonly known as biomass spectra

[1] Supplementary data for this article are available on the our Web site (http://cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 4078. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

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Table 1. Framework describing four size spectrum indicators examined here, including their potential response to exploitation and the ecological interpretation of the indicator and response to fishing and biases.

Indicator	Expected response to exploitation	Ecological interpretation	Biases
Linear slope	Decrease (steepens)	Relative abundance of large fish and loss of largest fish owing to size-selective fishery; potentially creates cultivation effect where small fish increase in number owing to release from predation by reduction in numbers of large fish	Reflects catchability of gear at largest and smallest sizes. Morphologies of fish (e.g., length of eel vs. lumpfish) are not always comparable size indicators. Because of equal length bins, sampling power is quite different between bins.
Parabola curvature	Equivocal	Predator–prey body size ratio and specific production: limbs of quadratic can change in same directions because of loss of large fish and increase in small fish leading to a less sensitive and (or) interpretable indicator of fishing.	Regression residuals are less likely to reflect changes in size range endpoint gear catchability.
Body size at parabola vertex	Decrease	Biomass where the bulk of the community biomass is located (like a biomass mode), consequently changes will reflect important ecological alterations: decreases reflect fisheries deriving large yields from the sizes around the vertex	As with curvature.
Biomass at parabola vertex	Increase then decrease	Closely follows total community biomass: may increase in early years of exploitation as midsizes obtain more resource owing to competitive release from largest fish removed by new fisheries; with continued exploitation of the system, fisheries will more specifically target middle size classes leading to reductions in biomass.	As with curvature.

(Fig. 2*b*), three indicators were derived: curvature of the fitted parabola, body size at the parabola vertex, and biomass at the parabola vertex. The vertex coordinates of the parabola can be determined by fitting the quadratic in the form

$$f(x) = a(x - h)^2 + k$$

where the vertex coordinates are (h, k).

All data were prefiltered to include individuals of lengths between 15 cm and 150 cm, primarily to avoid problems with low catchability of fish smaller than 15 cm. Time series of the various size spectrum indicators are presented for each system. Additionally, we fitted linear models of indicator vs. time to show the general trends and to aid comparison between systems. If these models had a significant 1st-order residual autocorrelation error (5 of 24 models), then the linear model was refitted with an AR1 correlation structure. Fittings were conducted in S-PLUS 6.1 using the GLS (generalized least squares) function (Insightful Corporation 2002).

Total annual fisheries catch for each of these systems is presented, as this provides some indication of the level of fishing pressure, which is a prime driver in all these systems. We did not attempt to standardise catches as community exploitation or make direct year-to-year comparison with various metrics owing to nonlinear and (or) lagged community response and numerous other assumptions that could result in a misleading analysis. Total catch data are freely available as Fishstat databases (FAO; www.fao.org) or from NAFO (www.nafo.ca; spreadsheet format available as well for demersal fish only) for the western Atlantic and from ICES (www.ices.dk; Fishstat database only) for the North Sea (IVabc).

We created a qualitative framework for comparing the four size spectrum metrics analysed, their expected response to exploitation, the ecological interpretation of this, and their biases (Table 1). With more empirical and simulation work, it might be possible to come up with definitions of community status (e.g., sustainably fished or overfished) based on such indicators, though that is beyond the scope of this study. The scheme in Table 1 is to show how we expect indicators to change in response to fishing and ecologically why this is so.

Results

Northern Gulf of St. Lawrence

Various metrics were inconsistent in this system (Table 2; Fig. 3). That is, according to the scheme outlined in Table 1 and the ecological interpretation of these metrics, it is unclear what occurred in the northern Gulf system based on the 1990–2002 Needler summer survey. Slopes of indicator vs. time showed small increases for all but biomass at the parabola vertex. These results, especially the increase in body size (slope and vertex body size) from 1990 to 1995, are incon-

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Table 2. Temporal response of size spectrum indicators in different systems and the evaluation of system status derived from them according to the framework outlined in Table 1.

Indicator	Northern Gulf of St. Lawrence	Sydney Bight	Eastern Scotian Shelf	Western Scotian Shelf	Georges Bank	North Sea	Overall evaluation
Linear slope	Increase then decrease (0.0008)	Steepening decrease (–0.0019)	Decrease (–0.0023)	Decrease (–0.0008)	Decrease (–0.0037)*	Decrease (–0.0016)	Loss of large fish in most systems
Quadratic curvature	Level then increase (0.0039)	Decrease (–0.002)	Decrease then level (–0.002)	Increase then decrease (–0.0015)	Decrease then slight increase (–0.003)	Level then increase (–0.0017)*	Body size range expansion and contraction unclear
Body size at quadratic vertex	Increase then level (0.0666)	Steepening decrease (–0.046)	Decrease (–0.0478)*	Decrease (–0.0284)	Decrease (–0.0576)*	Decrease (–0.1952)	Decline in the most common body size by biomass
Biomass at quadratic vertex	Decrease then level (–0.0327)	Slight increase then decrease (–0.0235)*	Increase then decrease (–0.019)	Level then increase (0.0224)	Slight decrease (–0.025)	Slight increase (0.0214)	Little change (compensation) or decrease (overexploitation) with time

Note: Numbers in parentheses are the slopes of linear models fitted to indicator vs. time showing the overall temporal trend. Numbers followed by an asterisk (*) are the slopes resulting from a linear model fitted with a AR1 1st-order autocorrelation structure.

sistent with our knowledge of the fishery collapse leading to a moratorium on cod fishing in 1994. Although the model fits were generally good (Fig. 3, R^2 values as points in the figures), the interannual variability was quite large, suggesting that individual year effects are very strong for this survey and (or) fish community and this makes it difficult to determine temporal trends in the data. Catch (primarily cod, *Gadus morhua*, and redfish, *Sebastes* spp.) in this system declined approaching the 1994 moratorium and there were minor increases in catch, mostly cod after 1996 and turbot, *Reinhardtius hippoglossoides*, thereafter.

Sydney Bight

Body size (as linear slope and quadratic vertex) showed a continual decrease over time and a rapid decline in biomass at the vertex of the fitted quadratic after the mid-1980s (Fig. 4). Quadratic curvature showed a slight but noisy decline over the time period, suggesting a weak trend towards a reduced range of fish sizes in the system. The decrease in all indicators with time was greatest for vertex body size (Table 2). Demersal catch followed the biomass at the vertex in this system as in most other systems.

Eastern Scotian Shelf

Trends in this system were very similar to those of the Sydney Bight but more pronounced (Fig. 5). Body size sharply declined in the largest sizes (linear slope), as well as body size at the quadratic vertex representing the single size containing the most biomass, the latter showing the largest decrease over time (Table 2). The biomass at the vertex increased to peak in the mid-1980s and declined thereafter. This is a collapsed fishery production system as only small catches were recorded after 1992 consisting mostly of silver hake (*Merluccius bilinearis*).

Western Scotian Shelf

Body size, as both the linear size spectrum slope and body size at the vertex of the parabola, decreased in this community (Fig. 6; Table 2). Biomass at the vertex of the parabola was level until about 1980 and showed a noisy increase (resulting in an overall slight increase; Table 2) thereafter, suggesting that ecological processes buffered changes in total biomass resulting from fisheries. According to the scheme in Table 1, indicators suggest that this system is relatively healthy (or similar to early years in the series) from a community body size perspective. Demersal fish catch from this community was fairly constant until about the mid-1980s and declined thereafter to about 25%–50% of the mean pre-1985 catch level.

Georges Bank

Body size showed a decreasing though variable trend over time (Fig. 7; Table 2), measured as both size spectrum slope and vertex body size. Biomass at the quadratic vertex was variable and showed only a slightly decreasing trend over the time series, suggesting, according to the Table 1 scheme, that fisheries and other disturbances have not much affected the amount of biomass in the middle sizes even if species composition did change. After about 1991, interannual variability in both linear slope and quadratic curvature (departure about smoother Fig. 7) increased.

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Fig. 3. Temporal trend in four size spectrum indicators for the northern Gulf of St. Lawrence trawlable fish community and fishery yield: (*a*) length–frequency spectrum slope; (*b*) biomass spectrum quadratic curvature; (*c*) $\log_2$ body size at parabola vertex; (*d*) $\log_2$ biomass at parabola vertex; (*e*) total reported fisheries catch (tonnes, from NAFO). Points appearing as numbers are the r^2 values of the regression fitting. Lines are spline smooths to show trends.

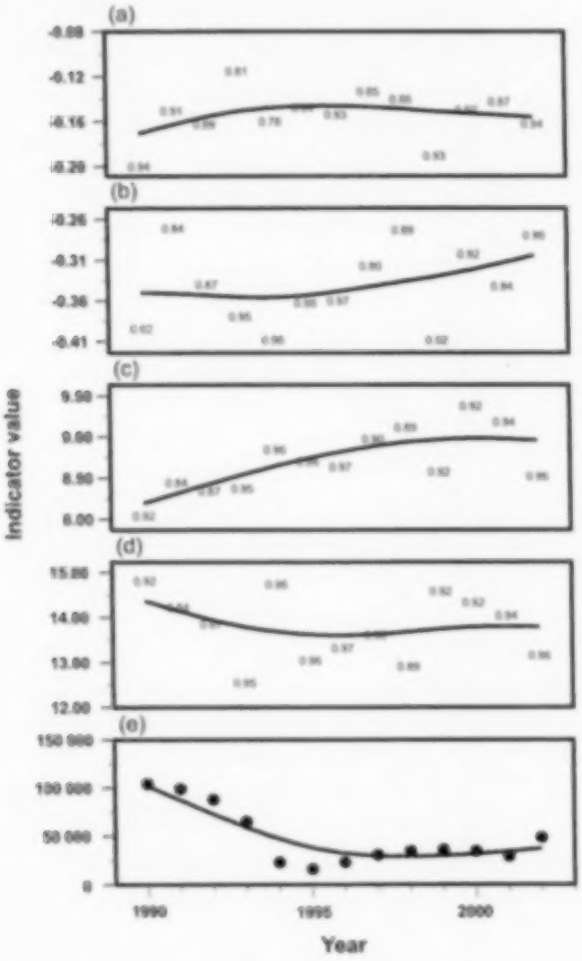
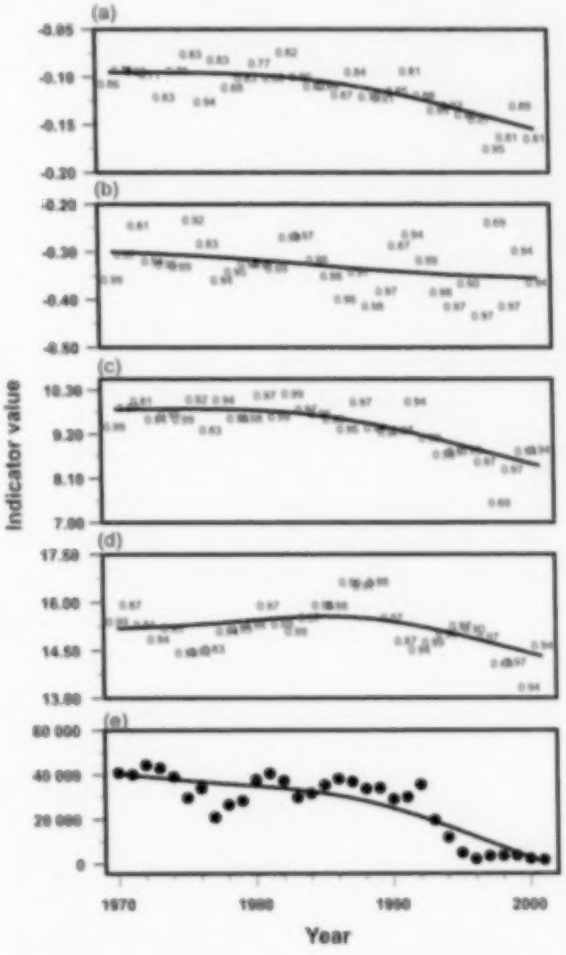


Fig. 4. Temporal trend in four size spectrum indicators for the Sydney Bight trawlable fish community and fishery yield: (*a*) length–frequency spectrum slope; (*b*) biomass spectrum quadratic curvature; (*c*) $\log_2$ body size at parabola vertex; (*d*) $\log_2$ biomass at parabola vertex; (*e*) total reported fisheries catch (tonnes, from NAFO). Points appearing as numbers are the r^2 values of the regression fitting. Lines are spline smooths to show trends.



North Sea

Body size for the North Sea fish community decreased by both measures, whereas biomass at the quadratic vertex showed a small increase over time (Fig. 8; Table 2). This is a situation similar to that of Georges Bank. Body size at the vertex in 1995 was very small because of the appearance of a large abundance of blue whiting, *Micromesistius poutassou*, and the fitted quadratic curvature increased (widened) to accommodate the presence of these relatively small fish. This indicator can therefore be quite sensitive to strong recruitment events in the North Sea. The slope of the linear model fitted to curvature vs. time was negative when 1st-order residual autocorrelation was accounted for in the model, even though the trend appears to be increasing. This suggests a flip-flop behaviour for this indicator in the North Sea demersal fishes. Most metrics showed more interannual variability after about 1990 (r^2 values in Fig. 8). This may be a result of changes in the English Groundfish Survey design in the early 1990s, which may have changed catchability properties. Total fisheries catch in the North Sea since the mid-1980s has remained at a level near 2×10^6 tonnes·year^{-1}.

Discussion

Various size spectrum measures provide complementary information on the state of systems. For example, the linear size spectrum slope is indicative primarily of the decline in

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Fig. 5. Temporal trend in four size spectrum indicators for the eastern Scotian Shelf trawlable fish community and fishery yield: (*a*) length–frequency spectrum slope; (*b*) biomass spectrum quadratic curvature; (*c*) $\log_2$ body size at parabola vertex; (*d*) $\log_2$ biomass at parabola vertex; (*e*) total reported fisheries catch (tonnes, from NAFO). Points appearing as numbers are the r^2 values of the regression fitting. Lines are spline smooths to show trends.

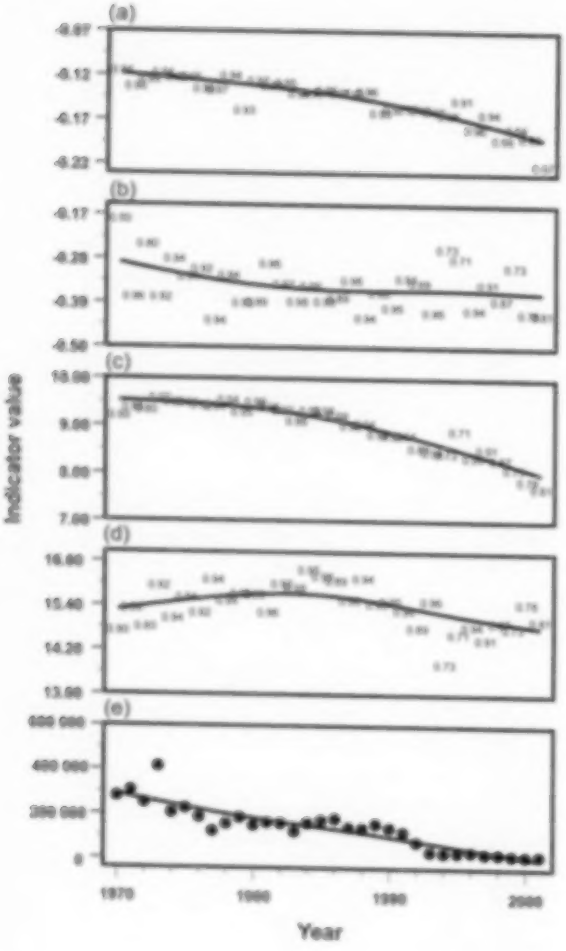
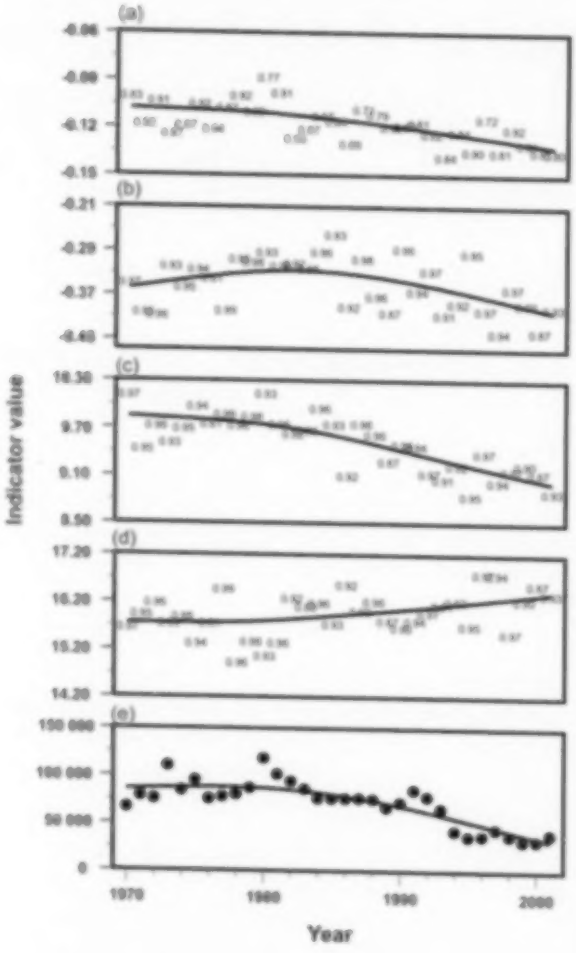


Fig. 6. Temporal trend in four size spectrum indicators for the western Scotian Shelf trawlable fish community and fishery yield: (*a*) length–frequency spectrum slope; (*b*) biomass spectrum quadratic curvature; (*c*) $\log_2$ body size at parabola vertex; (*d*) $\log_2$ biomass at parabola vertex; (*e*) total reported fisheries catch (tonnes, from NAFO). Points appearing as numbers are the r^2 values of the regression fitting. Lines are spline smooths to show trends.



abundance of the larger fish in a system (Pope et al. 1988), which has declined in all of the studied systems. The body weight at the vertex of a quadratic fitted to biomass spectra, however, not only reflects the abundance of large fish in the system, but also the body size of fish where the community biomass peaks; hence, vertex body weight is a biomass-weighted mode. These are different pieces of information with different sensitivities to perturbation and biases. The linear slope is quite sensitive to abundance of large and small fish, rather than to body size where the bulk of the ecologically active biomass is located. Consequently, linear slope is likely more sensitive to gear and vessel changes than is body size at the parabola vertex. This is because survey changes are more likely to affect the catchability of fish at the endpoints of the sampled size range (e.g., Trenkel et al. 2004; ICES 2005), whereas the midrange body size is more likely to be well sampled by most gears.

Biomass at the parabola vertex is a reflection of the biomass at the most common (as measured by biomass) body size in the community. Though not shown here, the vertex biomass value is very closely correlated with total survey biomass as a large proportion of the surveyed biomass comes from these intermediate body sizes. The parabola vertex is akin to total biomass or numbers in a similar manner to the linear size spectrum intercept (Sprules and Munawar 1986). The intercept often shows an increase with fishing and as slope decreases (Bianchi et al. 2000, which has sometimes been attributed to a cultivation effect (Walters and Kitchell 2001) where decreased abundance of large predators leads to increases in abundance of small prey fish. There

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Fig. 7. Temporal trend in four size spectrum indicators for the Georges Bank trawlable fish community and fishery yield: (*a*) length–frequency spectrum slope; (*b*) biomass spectrum quadratic curvature; (*c*) $\log_2$ body size at parabola vertex; (*d*) $\log_2$ biomass at parabola vertex; (*e*) total reported fisheries catch (tonnes, from NAFO), catch data from the USA after 1993 is not included. Points appearing as numbers are the r^2 values of the regression fitting. Lines are spline smooths to show trends.

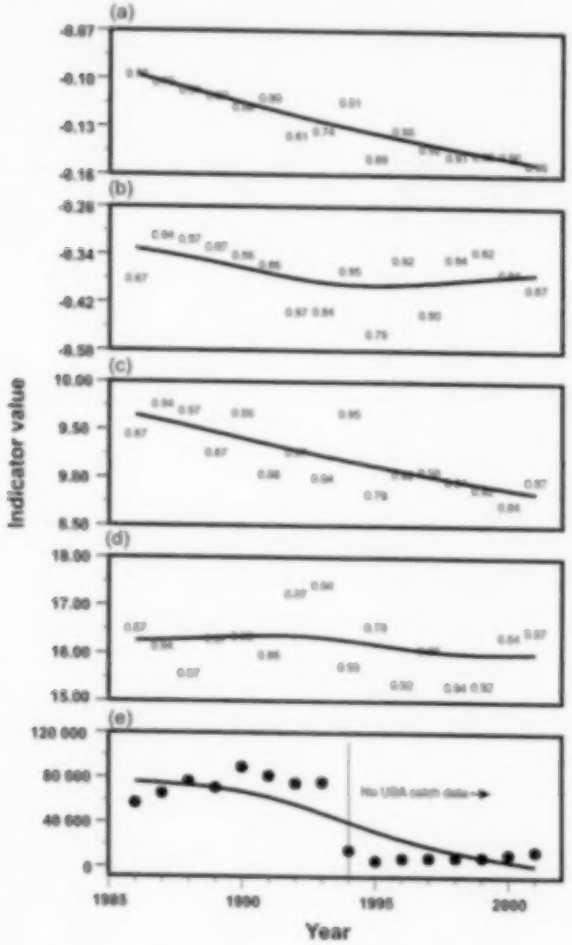
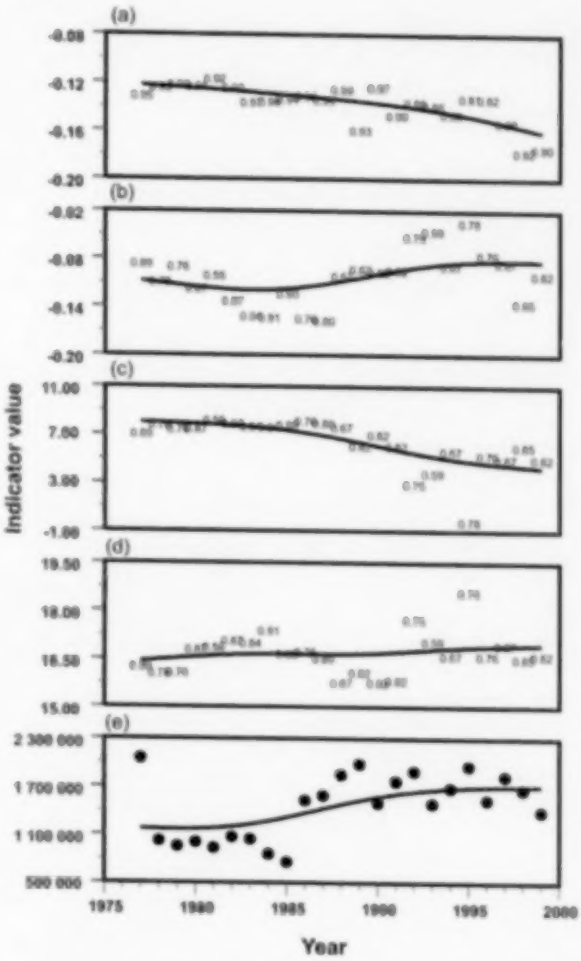


Fig. 8. Temporal trend in four size spectrum indicators for the North Sea trawlable fish community and fishery yield: (*a*) length–frequency spectrum slope; (*b*) biomass spectrum quadratic curvature; (*c*) $\log_2$ body size at parabola vertex; (*d*) $\log_2$ biomass at parabola vertex; (*e*) total reported fisheries catch (tonnes, from ICES). Points appearing as numbers are the r^2 values of the regression fitting. Lines are spline smooths to show trends.



may be a cultivation effect in the North Sea (Daan et al. 2005), but in most other systems, adequate analyses have not be conducted to verify the effect. Because the linear size spectrum intercept is usually strongly correlated with the slope, an apparent cultivation effect may be a statistical artefact of fitting the straight line. Unless the intercept is centred (referred to as "height"; Daan et al. 2005), it is difficult to determine if a cultivation effect has occurred. The biomass at the parabola vertex, however, is like the height of the straight line fitted to length–frequency spectra and may more readily reveal release in competition or predation owing to declines in large fish abundance.

It is not clear ecologically what quadratic curvature reflects in these systems. Theoretical work suggests that curvature reflects a combined effect of changed predator–prey size ratio and production–biomass ratio (Thiebaux and Dickie 1993), though it is difficult to disentangle those two parameters to make ecological inferences without fixing one of the parameters (Duplisea and Kerr 1995). Certainly, decreases in curvature reflect a parabola fit over a smaller range of body size, but one could describe situations where body size range decreases or increases for a variety of reasons that may be unrelated to fishing, e.g., recruitment events or growth of fish to a large size owing to low exploitation in unfished systems combined with poor recruitment. The latter could be a partial explanation for the increase in curvature value in the northern Gulf of St. Lawrence after the fisheries moratorium imposed in 1994. Long-term sustained changes in curvature may reflect changes in the system resulting

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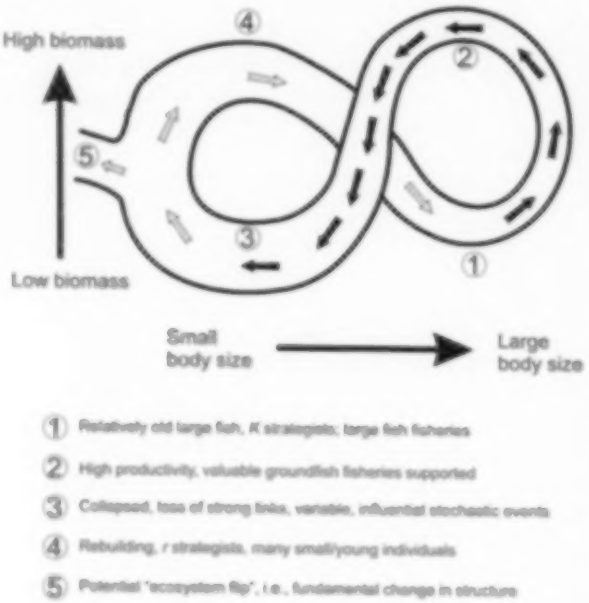
from increased or decreased abundance of species with very large or very small adult body size.

Body size at the parabola vertex will be sensitive to data that move the fitted parabola vertex outside the sampled body size range. This can occur if large recruitment events arise in a system over several size classes, which is probably what is represented by the low vertex body size in 1995 in the North Sea where abundance of fish <130 g was quite high compared with that in other years. The concomitant increase in curvature in 1995 reflects not only the shift in the parabola position, but also its widening to accommodate the large abundance of small fish. The original steady state theory for fitting parabolas (Thiebaux and Dickie 1993) and empirical fits (Sprules and Goyke 1994) have suggested that only horizontal and vertical shifts in parabola vertices, though not changes in curvature, should occur across broad groups such as phytoplankton, zooplankton, and fish. This work for communities far from steady state shows that concomitant shifts and changes in curvature are likely indicative of nonequilibrium events such as large recruitment events in the system. Therefore, although quadratic curvature is difficult to interpret, large interannual changes in its value can suggest the occurrence of an event beyond what steady state theory predicts, and this is useful to interpret why large changes in the body size at the vertex may occur.

Different size spectrum indicators usually reflect different aspects of the community response to exploitation; therefore, by combining indicators we are likely to develop a more complete indication of community state. For example, the biomass at the vertex of a fitted parabola concomitant with a decrease in body size at the vertex suggests that a fishery may be taking more than the community surplus yield, i.e., exploitation that leads to decrease not only in community body size, but also in biomass. Vertex biomass is likely to increase in early stages of exploitation owing to competitive release of resources as fisheries target the largest fish in the system; however, continuing fisheries usually begin to target smaller individuals and the biomass will begin to decline in intermediate sizes if yield exceeds surplus production. When both the body size and biomass positions of the vertex are decreasing, essentially there is a situation in which the community is overfished, i.e., surplus production is surpassed and fisheries begin to target ever smaller sizes to maintain yields. This is a different casting of the concept of "fishing down food webs" (Pauly et al. 1998). If we are to eventually define community or ecosystem sustainability and overfishing (Link and Brodziak 2003), it will most likely come about through combining various indicators of the fish community.

The large decline in both body size and biomass of the biomass spectrum vertex along with low recent fisheries yield for the eastern Scotian Shelf suggest that it is a "collapsed" fish production system. Relatively large fish catches were taken in the mid-1980s at a time when biomass spectrum vertex biomass was maximised and body size was still relatively large. Such a situation might be considered an optimum community configuration for maximising use of the fish production system. Unfortunately, this pattern does not appear to be universal; however, no other system studied has collapsed so clearly as the eastern Scotian Shelf (Frank et al. 2005), where cod biomass is practically undetectable in recent years (Canadian Science Advisory Secretariat 2003), predatory grey seal (*Halichoerus grypus*) abundance is very high, and water cooled in the 1990s (Fu et al. 2001; Choi et al. 2004).

Fig. 9. The "lazy-8" from Holling (1992) modified to represent the situation for an exploited temperate/boreal marine fish community as depicted by size spectrum parameters. The closeness of the arrows represents the rate of change in state; the solid arrows represent the states that have been observed (eastern Scotian Shelf), and the shaded arrows are hypothetical and have not been observed. The width of the path in stages 3 and 4 represents the large variability of the size structure then and the potential to occupy a much larger range of possibilities in state than at stages 1 and 2. The eastern Scotian Shelf, the most changed or collapsed system, would be in the lower left part of the diagram.


High biomass
Low biomass
Small body size
Large body size
1
2
3
4
5
1 Relatively old large fish, K strategists, large fish fisheries
2 High productivity, valuable groundfish fisheries supported
3 Collapsed, loss of strong links, variable, influential stochastic events
4 Rebuilding, r strategists, many small/young individuals
5 Potential "ecosystem flip", i.e., fundamental change in structure

The pattern for the eastern Scotian Shelf is reminiscent of the four stage pattern of (*i*) exploitation, (*ii*) conservation, (*iii*) release, and (*iv*) reorganisation in ecosystems described by Holling (1992), subsequently termed the "lazy-8" as the pattern resembles the figure "8" turned on its side. That is, we can view a modified lazy-8 (reflected on a horizontal axis) in biomass spectrum vertex space (vertex body size vs. vertex biomass), though not completely horizontal (lazy) (Fig. 9). This speculative casting of the lazy-8 for size spectra suggests that fisheries and other disturbances will reduce the abundance of large fish, subsequently leading to a decline in competition such that smaller (yet still commercially exploitable) fish increase in biomass. Ultimately the community decline in biomass and body size is defined as a collapsed state. The community may then rebuild to the previous state following a sequence that is not merely a reversal of the decline, or it may switch to an alternate state. The numbered stages in Fig. 9 correspond to Holling's numbered stages such that Fig. 9 stages 1, 2, 3, and 4 correspond

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to Holling's stages 2, 3, 4, and 1, respectively. If a fish community does respond in a similar manner to the process outlined, which may be true for at least the eastern Scotian Shelf demersal fish community (presently in lower left area of the diagram), then there are several caveats of which we should be aware relating to management and recovery of exploited fish communities. (*i*) Exploitation is a disturbance to which a fish community is resilient to a point but can and will collapse if pushed too far (Duplisea and Blanchard 2005). Though this is obvious, it takes on a greater meaning in the context of Holling's lazy-8. (*ii*) Community biomass can be optimally exploited at the intersection of maximum biomass and modal body size. (*iii*) Fish community recovery after collapse may not be directly reversible, but there are hysteretic (hysteresis) effects that may be both counterintuitive and undesirable. (*iv*) This suggests that all areas in multi- and single-species biomass space may not be able to be occupied in both directions (nonreversibility), contrary to current assumptions of stock management approaches. (*v*) A collapsed fish community is more susceptible to random influence such that it may switch to alternative community configurations and therefore never recover to a previous state regardless of the management action. (*vi*) Given the two previous points, risk management of fisheries with reference points should be highly risk averse in relation to limit reference points, as we are not sure that all the space between current stock state and the limit reference point can be occupied, i.e., single-species reference points may not be approachable continuously.

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Stable isotopes as an indicator of diet in omnivorous crayfish (*Pacifastacus leniusculus*): the influence of tissue, sample treatment, and season

Patrik Stenroth, Niklas Holmqvist, Per Nyström, Olof Berglund, Per Larsson, and Wilhelm Granéli

Abstract: Stable isotopes have been used to analyse food webs and (or) trace movements of animals for about 30 years. There has been some debate on the use of different tissues and treatments before isotope analysis, as well as on seasonal effects. We found different crayfish (*Pacifastacus leniusculus*) tissues (muscle, hepatopancreas, exoskeleton, gill, and whole body) to have different isotope values. Lipid extraction made whole-body carbon isotope values higher but had no effect on nitrogen isotope values. Acidification made whole-body isotope values lower. For crayfish, there was no seasonal or interannual variation in isotope values. In contrast to studies based on gut content analysis, we found adult crayfish to be at least as carnivorous as young-of-the-year crayfish. Earlier studies often have assumed that each food source contributes both nitrogen and carbon in equal proportions. Omnivores do not fit easily into this view. We suggest that nitrogen and carbon in an organism could come from different sources. Adopting this view for a pond food web could render crayfish both predators and detritivores as crayfish prey on nitrogen sources (other invertebrates) and consume large amounts of detritus to satisfy their carbon demand.

Résumé : Il y a environ 30 ans qu'on utilise les isotopes stables pour analyser les réseaux alimentaires et (ou) suivre les déplacements des animaux. Le choix des divers tissus, les préparations antérieures à l'analyse isotopique et les effets saisonniers ont fait l'objet de nombreuses discussions. Dans notre étude sur l'écrevisse *Pacifastacus leniusculus*, les différents tissus (muscle, hépatopancréas, exosquelette, branchie et corps entier) ont des valeurs isotopiques différentes. L'extraction des lipides accroît les valeurs des isotopes de carbone dans le corps entier, mais reste sans effet sur les isotopes d'azote. L'acidification réduit les valeurs isotopiques du corps entier. Chez l'écrevisse, il n'y a pas de variation des valeurs isotopiques d'une saison à l'autre ou d'une année à l'autre. Contrairement aux analyses des contenus du tube digestif, notre étude trouve les écrevisses adultes au moins aussi carnivores que les jeunes écrevisses de l'année. Les études antérieures ont souvent présupposé que chaque source dans le régime alimentaire fournit du carbone et de l'azote en proportions égales. Les omnivores ne cadrent pas facilement avec cette supposition. Nous croyons que l'azote et le carbone dans un organisme peuvent provenir de sources différentes. Si nous appliquons cette interprétation à un réseau alimentaire d'étang, les écrevisses deviennent à la fois des prédateurs et des détritivores puisqu'elles font de la prédation sur les sources d'azote (les autres invertébrés) et consomment de grandes quantités de détritus afin de satisfaire leurs besoins en carbone.

[Traduit par la Rédaction]

Introduction

Ecologists frequently use naturally occurring stable isotopes to identify food sources that are assimilated by consumers. Stable isotopes can also aid in analysing food web connections, tracing movements of animals, or assessing physiological conditions of consumers (Gannes et al. 1997). Stable isotopes integrate food sources over time and reveal what the animal has eaten, or rather assimilated, over the last days, weeks, months, or even years, depending on the size and elemental turnover rate of the animal. Ideally, the relative contribution of each food to the formation of tissue can be estimated using mixing models (Phillips and Gregg 2001, 2003). This approach has been very fruitful when looking at the relative importance of two different and distinct carbon sources, e.g., C_3 or C_4 plants or allochthonous sources compared with autochthonous sources in aquatic environments (e.g., France 1996; Sponheimer and Lee-Thorp 1999). How-

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ever, using the commonly measured carbon and nitrogen isotopic ratios, it is only possible to calculate the exact proportions of a maximum of three different foods with distinct signatures.

Omnivory (predation on more than one trophic level) is prevalent in many aquatic food webs (e.g., Diehl 1993). The multitude of potential food sources consumed by omnivores causes difficulties for analysis of stable isotope data from highly connected food webs. In addition to this, there are numerous assumptions of mixing models that may be particularly difficult to meet when dealing with omnivores, e.g., equal proportions of C and N should be assimilated from each food source or corrected for if possible (Gannes et al. 1997). When evaluating food sources for large-bodied, long-lived omnivores, there are additional factors to consider that could affect the interpretation of the results, including selection of tissue type for analysis (e.g., Hobson et al. 1993; Doucett et al. 1999; Gaston and Suthers 2004) and preparation techniques such as acidification and lipid extraction (Bunn et al. 1995; Bosley and Wainright 1999; Sotiropoulos et al. 2004). Temporal variation in food intake and ontogenetic diet shifts associated with consumer size may also significantly affect isotopic values of consumers (Gu et al. 1994; Cabana and Rasmussen 1996; Grey et al. 2001).

In this study, we assess the relative importance of tissue type, preparation techniques, and temporal and size variation in consumers when analysing food webs based on isotope ratios in long-lived, large-bodied omnivores. We use signal crayfish (*Pacifastacus leniusculus*) as a model organism because they can reach weights of about 0.3 kg (P. Stenroth, unpublished data) and ages of 16 years (Belchier et al. 1998). Omnivory is widespread within crustacea, crayfish, shrimps, and even zooplankton are often found to be omnivorous (Sprules and Bowerman 1988; Pringle and Hamazaki 1998). Gut content analysis shows that crayfish readily consume detritus, macrophytes, periphyton, invertebrates, and fish (Whitledge and Rabeni 1996, 1997; Stenroth and Nyström 2003). Omnivores such as crayfish can have a large impact on habitat, community composition, and energy flow in aquatic food webs (Abrahamsson 1966; Polis and Strong 1996; Stenroth and Nyström 2003). In addition, crayfish can form dense populations in lakes, streams, and ponds where they sometimes totally dominate the invertebrate biomass (Abrahamsson 1966; Abrahamsson and Goldman 1970; Mason 1975). Thus, crayfish play a key role in many aquatic ecosystems as both consumers and prey (Nyström 2002).

Earlier stable isotope studies have come to a range of conclusions regarding the diet of crayfish. Authors sometimes suggest detritus as an important food source for crayfish (Bunn and Boon 1993; France 1996; Evans-White et al. 2001). Others suggest that invertebrates are the primary energy source for crayfish (Nyström et al. 1999; Parkyn et al. 2001; Hollows et al. 2002). Carbon-to-nitrogen ratios of different food sources are likely to influence the assimilation of carbon and nitrogen from each source (Phillips 2001). Using stable isotope data of carbon and nitrogen from signal crayfish sampled in a pond, we tested whether isotope data can be used to identify food sources used by omnivores such as freshwater crayfish. Specifically, we were interested in whether the nitrogen isotope value of omnivores reflects the isotope value of the nitrogen-rich foods consumed and if the carbon isotope value reflects the isotope value of the carbon-rich foods. Furthermore, even though crayfish of all sizes are able to feed omnivorously, there are indications of ontogenetic diet shifts in crayfish. According to gut content analyses, juvenile crayfish feed predominantly on zooplankton and invertebrates, whereas adult crayfish consume primarily large amounts of detritus and macrophytes (e.g., Mason 1975; Westman et al. 1992; P. Stenroth, unpublished data). If this apparent shift in diet is important to crayfish nutrition, then it should also be detectable in stable isotope values.

To further improve the resolution of isotope values obtained from large-bodied crustaceans, we tested whether isotope values differ between tissue types (exoskeleton, hepatopancereas, gills, chelae, and tail muscle) and treatment (acidification and (or) lipid extraction). We also determined the statistical power of our analysis to get an estimate of suitable sample sizes needed.

Materials and methods

Study sites

There are four different data sets used in this study. (*i*) Data from Simontorp pond was used for the comparison between crayfish samples prepared in different ways (no treatment, lipid extraction, acidification, or combined). Isotope data from the pond also served as an example of a food web and were used to assess nitrogen and carbon sources used by signal crayfish of different sizes. (*ii*) Stable isotope signatures of crayfish from the "19 lakes" (Table 1) were used to estimate the within-population variation in crayfish signatures. This enabled us to estimate the sample size needed to detect a true difference between means of two samples. In addition, crayfish from Lakes Bunn, Båtsjön, Hövern, Sommen, St. Nätaren, Tolgsjön, Vitavattnet, Ören, and Örsjön were used to compare the signatures of whole-body and muscle samples. Samples from the 19 lakes were collected in July and August 2001, and in addition, crayfish from Lake Hövern were collected also in August 2003. Crayfish from Lake Hövern were then used to compare crayfish signatures between years. (*iii*) Crayfish from Lakes Boren and Mellanjuten were collected in August 2003. These crayfish were used to determine any difference in isotope values between different crayfish tissues (exoskeleton, hepatopancereas, gills, chelae, and tail muscle). (*iv*) Crayfish from Lake Åsunden were collected in August and September 2003. These crayfish were used to determine any difference in isotope values between crayfish collected during different months.

Basic limnological data for the lakes are provided (Table 1). The Simontorp pond in southern Sweden (55.59°N, 13.57°E (WGS 84)) is eutrophic (total phosphorous 47 $\mu g \cdot L^{-1}$). The samples from the pond were collected on 5 and 6 May 2000. The pond has a dense population of signal crayfish (mean catch-per-unit-effort (CPUE), i.e., catch per trap and night, of about 45; see below), and the fishes present are crucian carp (*Carassius carassius*), sunbleak (*Leucaspius delineatus*), and a few stocked rainbow trout (*Oncorhynchus mykiss*).

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Table 1. Descriptive limnological data for the lakes included in this study. The first 19 lakes are the ones included when reference is made to "19 lakes".

	Location (WGS 84)								
Lake	°N	°E	Surface area (ha)	Mean depth (m)	pH	Total phosphorous (μg·L^{-1})	Total nitrogen (mg·L^{-1})	Secchi depth (m)	Chl *a* (μg·L^{-1})
Bergsjön	57.08	14.74	326	3.4	6.43	31	0.79	0.8	20.7
Bunn	57.94	14.53	1 018	6.4	7.6	19	0.56	2.9	4.9
Bysjön	58.19	15.97	93	No data	7.3	58	0.95	0.9	41.1
Båtsjön	58.16	16.15	116	No data	9.4	93	1.55	0.55	85.0
Getryggen	58.18	16.08	20	No data	9.2	44	1.14	0.75	42.8
Helgasjön	57.00	14.77	5 067	6.1	6.8	15	0.53	2.2	11.5
Horsfjärden	58.15	15.91	381	12	6.5	8	0.33	6.5	3.0
Hövern	58.34	16.09	662	6.2	7.3	16	0.54	2.4	4.0
Nätaren	57.76	14.59	259	3.7	8.8	45	1.16	1.3	16.5
Skirösjön	57.36	15.39	118	5.2	7.1	42	0.86	1	19.3
Skärlen	57.17	14.85	329	8.4	6.6	5	0.33	7.7	3.2
Sommen	58.13	14.98	15 674	16.7	8.3	21	0.44	4.9	4.1
St. Nätaren	57.80	14.55	756	4.2	8.5	30	0.85	1.5	15.2
Tolgsjön	57.06	14.80	386	3	6.73	25	0.4	1.8	8.9
Vitavatten	56.26	14.58	39	8.6	6.32	6	0.29	6.8	1.8
Vättern	58.75	14.84	189 310	35	7.8	6	0.39	6	1.3
Växjösjön	56.86	14.81	87	3.35	7.9	54	0.83	1.3	20.0
Ören	57.94	14.58	917	13.5	8	12	0.43	4.9	2.9
Örsjön	56.46	13.95	493	2.1	6.38	17	0.54	2	8.7
Boren	58.88	15.15	2 730	No data	8.2	5	0.49	No data	5.3
Mellanjuten	58.83	15.81	182	No data	6.7	13	0.47	4	4.5
Åsunden	57.98	15.81	5 500	20	6.9	7	0.46	6	No data

Note: Chl *a*, chlorophyll *a*.

Organisms

Adult crayfish (>6 cm total length) were caught using baited cylindrical traps (cyprinid meat or commercial bait) (Edsman and Söderbäck 1999). Young-of-the-year and 1-year-old crayfish were netted in the littoral zone. All samples were frozen within 12 h of collection except adult crayfish from the Simontorp pond, which where put in a corf for 3 days to empty their guts before freezing. Crucian carp were caught using gill nets. Plankton nets were used to catch zooplankton (150 μm mesh size) and phytoplankton (<50 μm, >10 μm). Periphytic algae were scraped from stones near the shoreline. Invertebrates, except chironomids and *Sialis* sp., were caught by hand-netting in the littoral zone. Chironomids and *Sialis* sp. were caught using an Ekman grab at a depth of ~2 m. Detritus (of deciduous tree and macrophyte origins) was collected both in Ekman-grab samples and in the nearshore area.

Stable isotopes

Sample preparation

For crayfish, we either used whole-body samples or fresh samples of specific tissues. Whole-body samples of crayfish were freeze-dried to a constant weight. To compare muscle tissue signatures with whole-body signatures, about 10 mg (wet weight) of abdominal muscle tissue was withdrawn before freeze-drying. For this a total of 51 crayfish from nine different populations were used. Whole-body samples from 10 crayfish were divided into subsamples and used to examine the effects of different sample treatments, i.e., lipid extraction and acidification to remove carbonates. Subsamples of each dried crayfish were either ground to a fine powder directly or subject to Soxhlet extraction according to Bremle et al. (1995) and ground afterwards. For all ground samples, subsamples containing approximately 0.2 mg of organic carbon were put into tin capsules and subsequently used in stable isotope analysis. To produce acidified samples, we added 0.02 mL of 1 mol·L^{-1} HCl to each tin capsule with ground crayfish powder and the samples were then left to dry at 60 °C overnight. For all other samples, small pieces of fresh tissue (~0.2 mg of carbon) were used as samples. Pieces of the dissected tissue, muscle and other tissues, were put in tin capsules and dried at 60 °C for at least 1 h. Invertebrate samples were prepared from individual invertebrate abdomens. Each zooplankton sample contained five individual plankton.

Measuring the isotope signatures

Samples for determining isotope values were combusted in an ANCA-GSL preparation module (PDZ Europa Ltd., Sandbach, Cheshire, UK). Isotopes were analysed with a 20–20 stable isotope analyser (PDZ Europa Ltd.). The δ notation is the relative difference in isotope ratio between the samples and known standards as explained by the following equation:

$$\delta X = ((R_{sample}/R_{standard}) - 1) \times 1000$$

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where X is either ^{13}C or ^{15}N and the corresponding ratio is either $R = {}^{13}C/{}^{12}C$ or $R = {}^{15}N/{}^{14}N$. Vienna Pee Dee Belemnite is used as the standard ratio for carbon, and atmospheric nitrogen is used as the standard ratio for nitrogen. Glycin was used as internal standard, and the range for $\delta^{15}N$ readings was 0.8 ($n = 67$) and the corresponding value for $\delta^{13}C$ was 0.7. All isotope ratios are given in per mil (‰).

Mixing model

We used the mixing model provided by Phillips and Gregg (2001; version 1.04) to estimate the proportions of different food sources contributing to the isotope signature of crayfish in the Simontorp pond. We used 3.4‰ as the fractionation factor for nitrogen and 0‰ for carbon. The model is available at http://www.epa.gov/wed/pages/models.htm. We used the model under some different assumptions. Specifically, we tried to evaluate the effect of using the signature from either acidified or only dried crayfish samples on calculated contributions from different food chains. To do this we used both carbon and nitrogen isotope values in a three-source model. Sources were pooled values representing the periphytic, phytoplanktonic, and detrital food chains. The isotope values used for the periphytic food chain were the isotope values of periphyton. The corresponding values for the phytoplanktonic food chain were means of the values from chironomidae, phytoplankton, and zooplankton. The isotope value used for the detrital food chain was calculated as a mean of the values of all other potential food sources included in this study. We also examined the effect of using either the nitrogen value only or the carbon value only to calculate the contribution of different food chains to crayfish nutrition. When doing so we omitted the phytoplanktonic food chain and used a two-source mixing model. The phytoplanktonic food chain was omitted as it was calculated to contribute the least to crayfish nutrition in the three-source model. In addition, other macroinvertebrates than chironomids are often reported to be preferred prey for crayfish in lentic habitats (Dean 1969; Momot et al. 1978; Hessen and Skurdal 1986).

Statistical analysis

The relationship between standard deviation, sample size, and the size of the true mean difference likely to be detected was examined using Russ Lenth's power and sample-size page (http://www.stat.uiowa.edu/~rlenth/Power/). Data for statistical analysis were not transformed. This decision was guided by the fact that Lilliefors tests never showed data to differ significantly from normality. Paired-samples t tests were used to examine the difference between the signatures of whole-body and muscle samples. One-way analyses of variance (ANOVAs) were used to examine (*i*) the temporal variation in crayfish isotope signatures and (*ii*) the effect of the different treatment combinations of lipid extraction and acidification as both treatments had an effect on carbon isotope values. Two-way ANOVAs were used to examine (*i*) the effect of tissue and lake origin of samples on crayfish isotope values, (*ii*) effects of lipid extraction and acidification on whole-body samples, and (*iii*) the influence of sex and age or size on crayfish isotope values. Because we did not detect any differences between sexes or between crayfish older than 1 year, these crayfish were pooled. After pooling, t tests were used to compare the signatures of 0+ to older crayfish. Tukey's post hoc tests were used in association with ANOVAs. Statistical analysis was performed using SPSS 11.0.2 for Mac OS X (SPSS Inc. 2003).

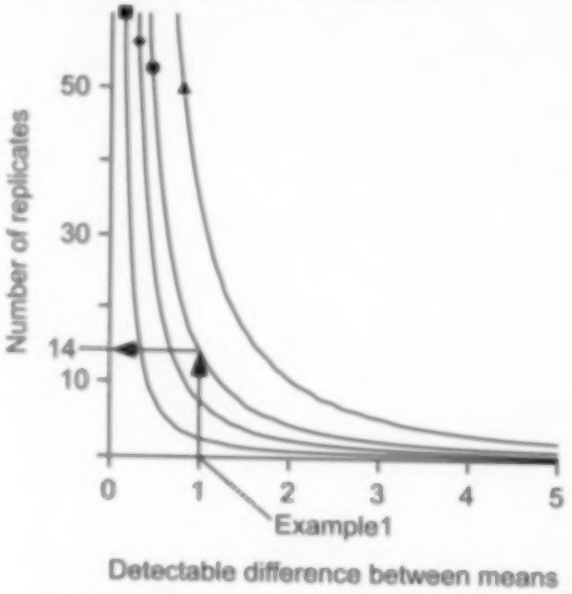

Fig. 1. Number of replicates needed to have an 80% chance of detecting a true difference between means of two samples, given equal variance. The curves represent different levels of variation within the samples; all exemplified standard deviations (SD) are found within crayfish (*Pacifastacus leniusculus*) populations. For the curve with the square, 1 SD = 0.3; the diamond denotes 1 SD = 0.6; the circle denotes 1 SD = 0.9; and the triangle denotes 1 SD = 1.5. Example 1: to detect a difference of 1 (in our case, ‰), a sample size of 14 is needed given that 1 SD = 0.9, a variation close to the mean variation in isotope signature in our crayfish populations. Sample sizes are calculated using Russ Lenth's power and sample-size page (http://www.stat.uiowa.edu/~rlenth/Power/).

Results

Sample sizes

The standard deviation of both nitrogen and carbon isotope values within crayfish populations (muscle samples) from 19 Swedish lakes varied from 0.27 to 1.82, with a mean of 0.88. The number of crayfish analyzed varied between 13 and 20 per lake. Thus, if it were assumed that a 1‰ difference in isotope values is ecologically important, a sample size of about 14 crayfish would be needed to have an 80% chance of finding a difference when comparing two populations with an average within-population variation (Fig. 1).

Choice of tissue

The signatures of muscle tissue versus whole-body samples were compared in nine lakes. For nitrogen, signatures were on average 0.9‰ higher in muscle tissue than in the whole-body samples (paired-samples t test, $n = 51$, $t_{50} = -8.434$, $P < 0.001$; Fig. 2). Somewhat counterintuitive, as inorganic carbonates are incorporated in the exoskeleton, we could not

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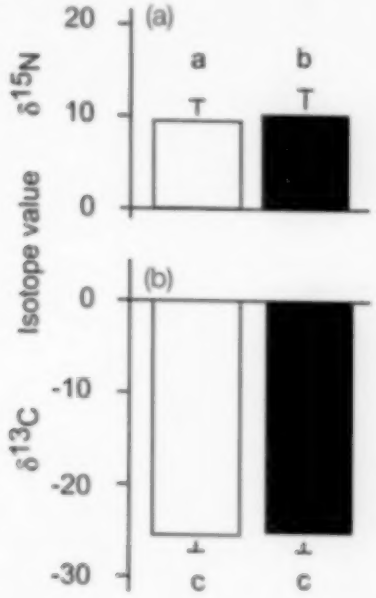
Fig. 2. Isotope signatures of whole-body samples (open bars) compared with muscle tissue samples (solid bars) of crayfish (*Pacifastacus leniusculus*): (*a*) $n = 51$ for nitrogen; (*b*) $n = 49$ for carbon. Height of bars and error bars (error bars represent 1 standard deviation) refer to measured isotope signatures, whereas letters above or below bars refer to paired-samples t tests. Different letters represent a significant difference at the 0.001 level. Crayfish originate from nine Swedish populations (5 or 6 crayfish per population).



detect any difference in carbon δ value (paired-samples t test, $n = 49$, $t_{48} = 0.931$, $P = 0.356$) between muscle and whole-body samples. However, a comparison of the isotope signatures of tail muscle, claw muscle, gills, hepatopancreas, and exoskeleton from two lakes showed significant differences in both nitrogen and carbon signatures between tissues (two-way ANOVA: nitrogen, $F_{[4,31]} = 52.240$, $P < 0.001$; carbon, $F_{[4,31]} = 79.112$, $P < 0.001$). For nitrogen, post hoc tests revealed that muscle tissue from tail or claws has a higher value than hepatopancreas, gills, and exoskeleton (Fig. 3), whereas the exoskeleton has a significantly lower value than the other tissues. For carbon, the $\delta^{13}C$ value of the exoskeleton was significantly higher, whereas the value of the hepatopancreas was lower than that of other tissues. Furthermore, there was a general difference between lake populations (two-way ANOVA: nitrogen, $F_{[1,31]} = 254.9800$, $P < 0.001$; carbon, $F_{[4,31]} = 748.823$, $P < 0.001$). In addition to this, there was a significant interaction between tissue and lake for nitrogen (two-way ANOVA, $F_{[4,31]} = 5.913$, $P = 0.002$) but not for carbon ($F_{[4,31]} = 0.879$, $P = 0.492$).

Treatment of samples

To determine if the treatment of samples would have any effect on the isotope value assigned to organisms, we compared the isotope values of samples (dried and ground) with those that had been acidified to remove inorganic carbonates and (or) where the lipids had been extracted. There was a

Fig. 3. (*a*) Nitrogen and (*b*) carbon isotope signatures of specific tissue samples of crayfish (*Pacifastacus leniusculus*) from Lake Mellanjuten (open bars) and Boren (solid bars) ($n = 3$ for each bar, except for muscles and exoskeleton from Lake Mellanjuten where $n = 4$; $n = 1$ for nitrogen for gills from lake Boren). Error bars represent 1 standard deviation. Different letters above or below bars represent a significant difference at the 0.001 level (Tukey's post hoc test). The overall signatures are significantly different for the two lakes, and the significant interaction between lake and nitrogen signature is dependent on the strong enrichment of the muscle samples from Lake Boren, which is lacking in Lake Mellanjuten. Note the different scales on the nitrogen and carbon axes.

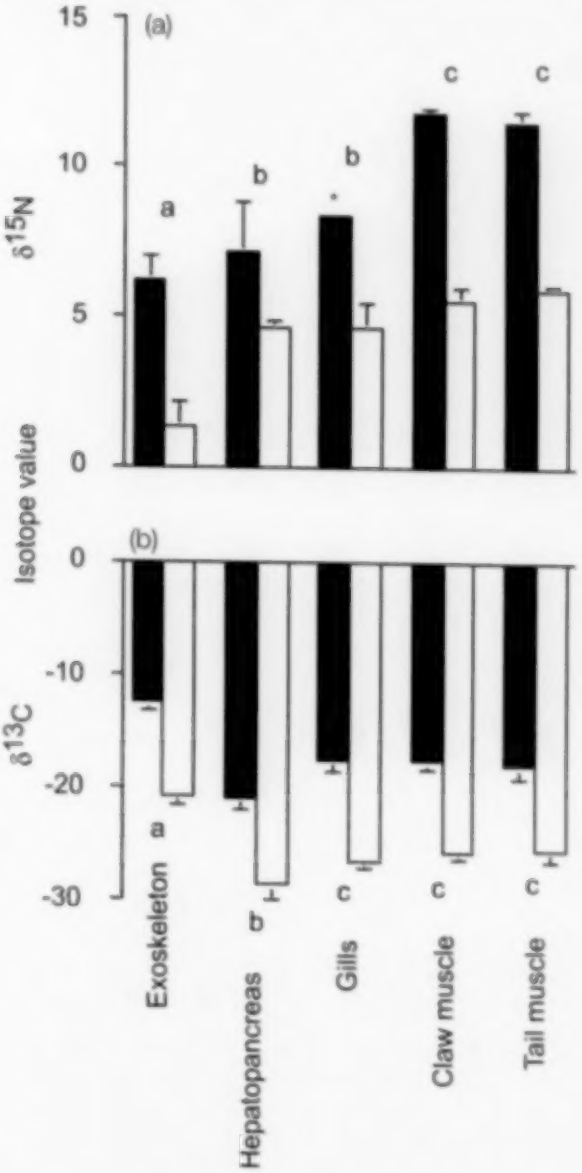


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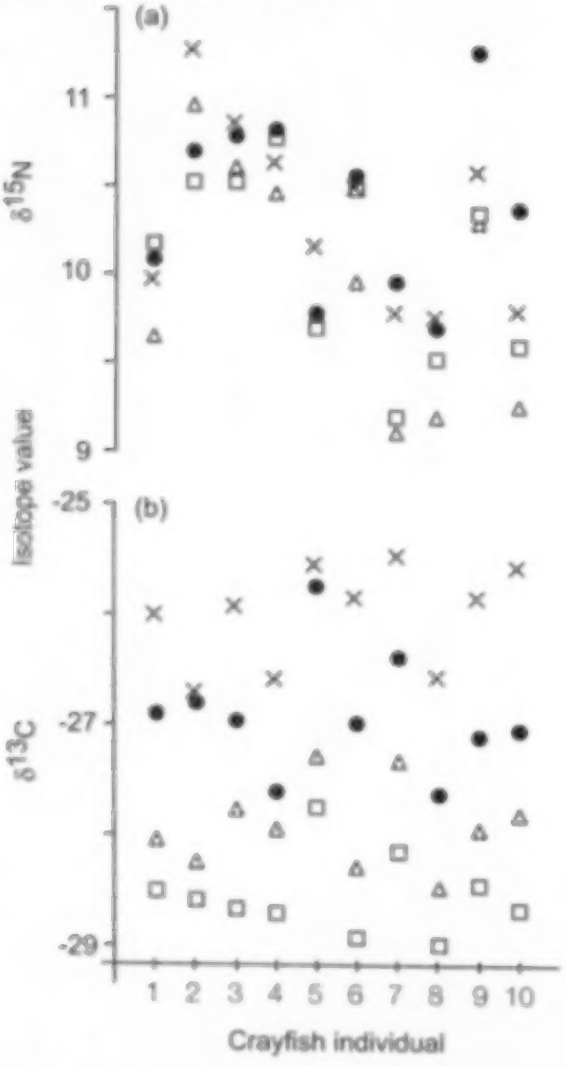
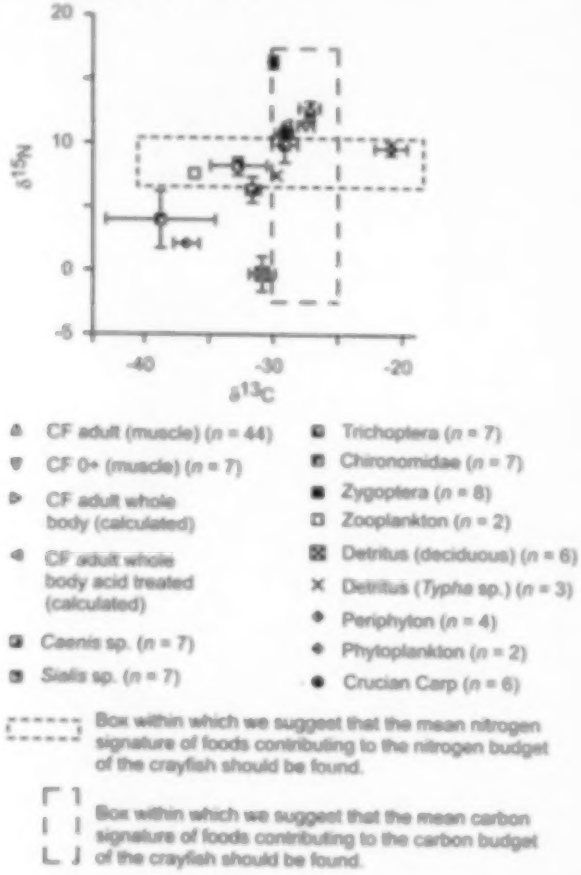
Fig. 4. (*a*) Nitrogen and (*b*) carbon isotope values of whole-body samples of 10 individual crayfish (*Pacifastacus leniusculus*) from Simontorp pond, where subsamples have been treated in different ways before oxidation in the mass spectrometer. Control samples were only dried and ground (solid circles). Crosses represent samples where lipids had been extracted, squares represent acidified samples, and triangles represent acidified samples where lipids had been extracted. Two-way analysis of variance showed that acidified samples had a lower nitrogen isotope value than nonacidified samples. For carbon, post hoc tests associated with a one-way analysis of variance showed that all treatments (including control) were different from each other. Note the different scales on the nitrogen and carbon axes.



significant effect of acidification on both nitrogen and carbon isotope values (two-way ANOVA: nitrogen, $F_{[1,36]}$ = 4.122, P = 0.05; carbon, $F_{[1,36]}$ = 155.753, P < 0.001; Fig. 4), whereas lipid extraction only affected the carbon isotope value (two-way ANOVA: nitrogen, $F_{[1,36]}$ = 0.471, P > 0.05; carbon, $F_{[1,36]}$ = 28.86, P < 0.001). We could not detect any interaction between acidification and lipid extraction. On average, an acidified sample had a nitrogen isotope value 0.4‰ ± 0.3‰ (mean ± 1 standard deviation, SD) lower than that of nontreated samples. For carbon, the corresponding value was 1.8‰ ± 0.3‰. Lipid extraction resulted in a 0.8‰ ± 0.4‰ increase in δ^{13}C values.

Fig. 5. Isotope values of crayfish (*Pacifastacus leniusculus*) and potential food sources, all collected in Simontorp pond. The isotope values of whole-body and whole-body acidified sample signatures are calculated using the results described in Figs. 2 and 4. Error bars represent 1 standard deviation. The long sides of the boxes represent the calculated signature for adult whole-body samples minus the mean fractionation factor ± 1.96σ (where σ refers to the fractionation factor population). Fractionation factors, etc., are according to Post (2002). Note the different scales on the nitrogen and carbon axes.


20
10
0
-5
δ15N
-40
-30
-20
δ13C
CF adult (muscle) (n = 44)
CF 0+ (muscle) (n = 7)
CF adult whole body (calculated)
CF adult whole body acid treated (calculated)
Caenis sp. (n = 7)
Sialis sp. (n = 7)
Trichoptera (n = 7)
Chironomidae (n = 7)
Zygoptera (n = 8)
Zooplankton (n = 2)
Detritus (deciduous) (n = 6)
Detritus (Typha sp.) (n = 3)
Periphyton (n = 4)
Phytoplankton (n = 2)
Crucian Carp (n = 6)
Box within which we suggest that the mean nitrogen signature of foods contributing to the nitrogen budget of the crayfish should be found.
Box within which we suggest that the mean carbon signature of foods contributing to the carbon budget of the crayfish should be found.

Temporal variation

To evaluate seasonal variation in δ^{13}C and δ^{15}N values in crayfish, we compared the isotope values of samples that were collected in different months but also in different years. We could not detect any difference in isotope value in crayfish between August and September samples from Lake Åsunden for either nitrogen or carbon (ANOVA, $F_{[1,40]}$ =

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Table 2. Estimated proportions of different food sources, using the mixing model of Phillips and Gregg (2001), contributing to the isotope values of the adult crayfish (*Pacifastacus leniusculus*) in Simontorp pond.

Whole-body crayfish isotope value used	Source food chain	Lower 95% CI	Estimated proportion contributing	Upper 95% CI	SE
Only dried	Detrital	0.17	0.44	0.71	0.13
	Phytoplanktic	0	0.13	0.27	0.07
	Periphytic	0.29	0.43	0.57	0.07
Acidified	Detrital	0.26	0.54	0.83	0.13
	Phytoplanktic	0.01	0.17	0.32	0.07
	Periphytic	0.15	0.29	0.43	0.07
Using only C	Detrital	0.58	0.65	0.43	0.04
	Phytoplanktic	Fixed at 0	Fixed at 0	Fixed at 0	Fixed at 0
	Periphytic	0.26	0.34	0.42	0.04
Using only N	Detrital	0.31	0.95	1	0.25
	Phytoplanktic	Fixed at 0	Fixed at 0	Fixed at 0	Fixed at 0
	Periphytic	0	0.04	0.68	0.25

Note: Crayfish isotope values used are different estimated signatures of crayfish (whole-body and whole-body acidified sample signatures calculated using the results described in Figs. 2 and 4) resulting in different proportions of potential food sources estimated to be contributing. The signature used for the periphytic food chain is the signature of periphyton in Fig. 5. The corresponding value for the phytoplanktic food chain is a mean of the signatures from chironomidae, phytoplankton, and zooplankton. The signature used for the detrital food chain is calculated as a mean of the signatures of all other potential food sources included in Fig. 5. CI, confidence interval; SE, standard error.

1.532, $P = 0.223$, and $F_{[1,40]} = 0.116$, $P = 0.735$, respectively). However, a true difference in means of approximately 1.1 for nitrogen and 1.6 for carbon would have been required to have an 80% chance of detecting a difference given the standard deviation of the samples (1 SD was ~1.15 for nitrogen and 1.8 for carbon). Furthermore, we could not find any difference, even on a longer time scale. There was no detectable difference in isotope signature between samples of crayfish muscle tissue from Lake Hövern collected in 2001 and 2003 (ANOVA, $F_{[1,40]} = 0.823$, $P = 0.37$, and $F_{[1,40]} = 1.089$, $P = 0.303$, for nitrogen and carbon, respectively). For these samples, 1 SD was 1.35 for nitrogen and 1.23 for carbon. For likely detection of a difference, this corresponds to differences around 1.1.

Omnivory and stable isotope ratios within a crayfish population

The isotope values of crayfish aged 0+, 1+, and adults (all muscle tissue) from the Simontorp pond were measured. We could not detect any difference in isotope signature due to sex or age or size between 1-year-old crayfish and adult crayfish (two-way ANOVA: for sex influencing nitrogen signature, $F_{[1,40]} = 0.001$, $P > 0.05$; for age or size influencing nitrogen signature, $F_{[1,40]} = 0.01$, $P > 0.05$). Corresponding values for carbon were $F_{[1,40]} = 0.003$, $P > 0.05$, for influence of sex, and $F_{[1,40]} = 1.238$, $P > 0.05$, for influence of age or size. Thus, crayfish aged 1+ were subsequently pooled. Age-0+ crayfish displayed $\delta^{15}N$ values that were 1.4‰ lower than their older conspecifics (t test, $t_{48.582} = -17.95$, $P < 0.001$), but we could not detect any difference in carbon value (t test, $t_{49} = -1.065$, $P = 0.292$).

Plotting of the carbon and nitrogen signatures for crayfish foods, compared with the isotope signature of crayfish and the likely range of fractionation factors for crayfish ($1.48 \leq \Delta\delta^{15}N \leq 5.32$; $-2.16 \leq \Delta\delta^{13}C \leq 2.94$) (Post 2002), suggested detritus to be the most important ultimate carbon source (Fig. 5). In addition, invertebrates were suggested to be important nitrogen sources for crayfish as most food items slightly lighter than crayfish are of animal origin (Fig. 5). This interpretation does not rely on any coupling between the assimilated carbon and nitrogen, i.e., the crayfish could assimilate all the nitrogen from one type of food and all the carbon from a different food source.

We also used a mixing model (see Materials and methods) to calculate the relative contributions of different food groups to crayfish nutrition. Because of the large number of food sources, we had to pool foods so that only three sources remained. We chose to pool foods into detrital, phytoplanktonic, and periphytic food chains. The mixing model showed that 44% of the assimilates in crayfish (whole-body, adults) came from the detrital food chain. Furthermore, we examined the effect of acidification of samples on the outcome of the mixing model. The result was that the difference in isotope signature, between control and acidified samples of whole-body crayfish, could have profound effects on the analysis of food web structure. If the crayfish isotope values from acidified samples (acidified $\delta^{13}C$ values were 1.8‰ lower) was used as input data instead of the isotope values of nonacidified crayfish, the result was that 54% of the assimilates were suggested to come from the detrital food chain (Table 2). Further, it should also be noted that this result (the 10% change in contribution from the detrital food chain) from the mixing model is sensitive to the relative position between mixture and sources. A similar-sized alteration in crayfish isotope value could change the calculation of relative contributions much more dramatically. For example, if the acidified samples had been 1.8‰ higher, instead of 1.8‰ lower as in the given example, the difference of 1.8‰ would have lowered the contribution from the detrital food chain from 44% to an average of –3%!

In addition, we calculated the contribution from the detrital and periphytic food chains to the nutrition of crayfish under the assumption that the phytoplanktonic food chain does not contribute to the nutrition of benthic crayfish (Table 2).

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The assumption enabled us to compare an analysis based on the carbon signature only to one based on the nitrogen signature only. When the nitrogen signatures were the basis for the analysis, the contribution from the detrital food chain was 95%. In contrast, when the carbon signatures were the basis for the analysis, the contribution from the detrital food chain was only 65%.

Discussion

The most important results from this study are as follows. (*i*) Carbon and nitrogen sources for omnivores could potentially be viewed as decoupled. This could have profound effects on the interpretation of stable isotope data of food webs where omnivores are included. We suggest that invertebrates could be the primary nitrogen source and that detritus could be the ultimate carbon source for crayfish. (*ii*) There were effects of both lipid extraction and acidification on the isotope signature of samples. However, the importance of these differences must be judged from case to case. (*iii*) Whole-body and muscle tissue samples of signal crayfish had similar signatures, but muscle tissue was slightly more enriched with respect to nitrogen. Different tissues had distinct and, in some cases, different signatures with respect to both carbon and nitrogen. (*iv*) Adult crayfish are at least as carnivorous as young-of-the-year crayfish with respect to assimilated nutrients.

Sample size

Traditionally, researchers envision rather clear-cut differences when thinking of food webs and stable isotopes, e.g., the isotope signature of terrestrial plants is often expected to be very different from the signature of phytoplankton. This line of thinking has probably influenced the choice of hypotheses, sample size, or both (e.g., France 1996; Bosley and Wainright 1999; Nyström et al. 1999). However, a small difference in the true mean, large variation in samples, and the influence of temporal variability often hampers the usefulness of isotope data. In this study, we provide isolines for estimating the required sample sizes for a range of standard deviations often encountered in stable isotope ecology. It should be noted that the slope of the isolines is correlated to how much smaller a difference one extra sample will enable researchers to detect.

Choice of tissue and treatment of samples

Many food web studies based on stable isotopes use either muscle tissue, if the organisms are large enough (or if they are too large for whole-body samples), or whole-body samples when dealing with smaller organisms. Intuitively, one would expect larger differences between whole-body and muscle samples for the carbon isotope values than for nitrogen isotope values, as whole-body samples include fatty tissues such as the hepatopancreas (known to be isotopically light with respect to carbon) and, for crayfish, the exoskeleton that contains inorganic carbonates. However, we could not detect any difference in carbon isotope signature between whole-body and muscle samples. The contribution of the isotopically light hepatopancreas appeared to be balanced by the isotopically heavier exoskeleton and summed up to an isotope value similar to that of the intermediate muscle tissue. This is, of course, a special case for crayfish and potentially some other organisms that incorporate some inorganic carbonates from the water to the exoskeleton.

With respect to nitrogen, crayfish muscle samples were 0.8‰ higher than whole-body samples. It is not surprising to find a difference in nitrogen signature between the sample types. Other authors have also found that different tissues have different signatures (Hobson et al. 1993; Pinnegar and Polunin 1999). For crayfish, there does not seem to be any tissue heavier than muscle tissue, at least not to any larger extent. However, there does not seem to be a consistent pattern between species. For example, Hobson et al. (1993) found muscle tissue to be isotopically light compared with other tissues in Japanese quail (*Coturnix japonica*), whereas Pinnegar and Polunin (1999) found muscle tissue to be among the isotopically heaviest in rainbow trout (*Oncorhynchus mykiss*).

Because the differences between muscle and whole-body samples were rather small, either sample type could be used for exploring many of the more traditional questions regarding crayfish in stable isotope studies. For example, the contribution from terrestrial leaves to the nitrogen budget of crayfish in this study seems to be small, no matter what type of isotope samples are used. However, Lancaster and Waldron (2001) suggested that interspecific differences in the proportional contribution of different tissues might influence the whole-body signature of different animals. This effect can be important for some questions, even on an intraspecific level, for example, if one wants to test if the observations by Abrahamsson (1966) that large male crayfish displace females from the most productive feeding areas in the nearshore zone also are reflected in diet and isotope values of crayfish. As crayfish grow, the ratio between different tissues, e.g., muscle to whole body, changes (Stein and Murphy 1976; Huner et al. 1988). Furthermore, the ratios between different tissues sometimes differ between sexes (Huner et al. 1988). Thus, isotopic signatures of whole-body samples are likely to be size- and (or) sex-biased. If larger crayfish have a larger proportion of muscle tissue, as Huner et al. (1988) suggest, then whole-body samples of larger crayfish are likely to display higher values with regard to nitrogen. It is possible to come down with a 1‰ difference in nitrogen isotope value simply because of a 5% difference in muscle-to-weight ratio if you use whole-body samples. This potential difference in isotopic signature could erroneously be interpreted as evidence for a difference in diet. This problem is avoided if the samples are prepared from muscle tissue. However, it should be noted that Bittner and Traut (1978) reported direct proportionality between abdominal muscle and whole-body weight; if that were true for the species at hand, then muscle and whole-body samples would be equally suitable.

For carbon, the effects of acidification and lipid extraction are in accordance with other studies. Removal of lipid, known to be isotopically light (Pinnegar and Polunin 1999; Sotiropoulos et al. 2004), makes the samples isotopically heavier. Removal of inorganic carbonates, which are isotopically heavy (e.g., represented by the exoskeleton in Fig. 3), made the samples lighter. This is consistent with Bunn et al. (1995) who found a similar effect of acidification if, and only if, the exoskeleton was included in the samples. Others report a

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lack of effect, but then there is no partly inorganic exoskeleton included in the samples (Bosley and Wainright 1999; Pinnegar and Polunin 1999). For nitrogen, acidification made the samples isotopically lighter. The acidification procedure in this study differs from most others in one aspect: the samples were not flushed with water after the application of acid. Thus, it is unlikely that our result was dependent on a loss of a fraction of nitrogen. According to other studies, acidification makes nitrogen samples isotopically heavier (Bunn et al. 1995; Pinnegar and Polunin 1999), but these studies have used washing techniques that do not add the nitrogen solved by the acid used for washing to the subsequent sample.

To conclude, we recommend the use of untreated muscle tissue for most purposes in stable isotope ecology. However, obvious exceptions are to be found, such as when consumers preferentially utilize other tissues from their prey, e.g., bears that preferentially consume salmon roe that probably would have a signature different from the signature in muscle tissue.

Temporal variation

Temporal variation in isotope signatures has caused problems in analysing routes of energy flow through food webs including small animals (e.g., zooplankton) with fast turnover rates. In contrast, isotope signatures change more slowly in larger animals. Few have examined if there is any temporal variation in isotope values of crayfish. We report that no significant changes occurred over months or even years within two lakes. This could suggest that crayfish have a similar diet irrespectively of season and (or) year, but it could also suggest that crayfish muscle tissue has a turnover rate slow enough to mask any between-month differences in diet. No major changes in their environment were reported during this period, and we conclude that isotope values from crayfish seem to be stable over this time span.

Omnivory and use of stable isotopes

In using muscle tissue, we found that adult crayfish have slightly higher isotope values with regard to nitrogen compared with young-of-the-year conspecifics. This finding contradicts the traditional view of crayfish diet during growth where small crayfish are thought to be carnivorous and larger individuals are more detritivorous (Abrahamsson 1966; Mason 1975; Goddard 1988). We have to conclude that large (adult) crayfish in Simontorp pond were at least as (or slightly more) dependent on animal nitrogen as their younger conspecifics. Several authors have suggested that animal nitrogen is important for the nutrition of all crayfish (e.g., Momot 1995; Parkyn et al. 2001), but none has showed that adult crayfish are as dependent on animal protein in their diet as young-of-the-year crayfish.

Furthermore, we found a rather low variation in isotope signature in crayfish compared with other invertebrates. This could be explained by high mobility of crayfish. All crayfish will encounter roughly the whole spectrum of signatures from each food source (Lancaster and Waldron 2001). The effect of variation in signature of each food source on the crayfish signature will thus be attenuated as each individual crayfish consumes a large number of food samples from each important food source and assimilates these samples to a mean signature. The remaining sources of variation in the crayfish signature would then be either individual variation in fractionation factor or individual preferences for or ability to handle different food items. This is partly in conflict with the mixing model we have used (Phillips and Gregg 2001), but as it would impair only the estimate of the confidence interval for the proportions and not the mean proportion estimate, we find it reasonable to present the interval despite our speculations.

We used a traditional mixing model as an initial approach for our pooled food web. The results suggest that the detrital food chain contributes about half of the assimilates for crayfish. However, to use this mixing model, we had to assume that the different food sources contributed assimilates in similar C:N ratios. This might well have been a reasonable assumption if this study dealt with strict herbivores or carnivores. However, this assumption is severely violated when dealing with omnivores like crayfish. For example, the C:N ratio is about 3.4 times higher in detritus from alder leaves than in a mayfly, both known to be part of the crayfish diet. Furthermore, there may be differences in assimilation efficiency for different elements from different sources, and in addition, there may also be differences in fractionation when an omnivore consumes food sources as different as invertebrates or alder leaves (e.g., Koch and Phillips 2002; Phillips and Koch 2002; Robbins et al. 2002). Hence, traditional models do not seem to be applicable when omnivory is prevalent.

However, we believe that there might be another interpretation of the data and the dual isotope plot. We suggest that the differences in C:N ratio between food sources potentially could decouple the carbon and nitrogen sources. For omnivores, we find it reasonable that this is a better approximation than assuming proportional contribution of carbon and nitrogen from each source. In our special case, dealing with the omnivorous crayfish, plant material could contribute to the carbon budget and invertebrates could contribute to the nitrogen budget. This interpretation would be compatible with the findings of Momot (1995) and Parkyn et al. (2001), for example, and would ameliorate the apparent dichotomy between the results from gut content analysis and stable isotopes in crayfish research.

We suggest that carbon and nitrogen assimilated in the tissues of omnivores can come from different sources. This has effects on our perception of the trophic relationships of omnivores, i.e., they could be predators with respect to one element and detritivores with respect to another. We suggest that these nutrient-specific roles of crayfish and potentially also other omnivores should be considered in future studies. The use of different tissues and preparation techniques in stable isotope studies can influence the interpretations made. We recommend that some indication of the robustness of interpretations be provided in future isotope studies.

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Long-term trends of bloater (*Coregonus hoyi*) recruitment in Lake Michigan: evidence for the effect of sex ratio

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Abstract: Long-term population trends are generally explained by factors extrinsic (e.g., climate, predation) rather than intrinsic (e.g., genetics, maternal effects) to the population. We sought to understand the long-term population dynamics of an important native Lake Michigan prey fish, the bloater *Coregonus hoyi*. Over a 38-year time series, three 10- to 15-year phases occurred (poor, excellent, and then poor recruitment) without high interannual variability within a particular phase. We used dynamic linear models to determine whether extrinsic (winter and spring temperature, alewife predator densities) or intrinsic factors (population egg production, adult condition, adult sex ratio) explained variation in recruitment. Models that included population egg production, sex ratio, winter and spring temperature, and adult bloater condition explained the most variation. Of these variables, sex ratio, which ranged from 47% to 97% female across the time series, consistently had the greatest effect: recruitment declined with female predominance. Including biomass of adult alewife predators in the models did not explain additional variation. Overall our results indicated that bloater recruitment is linked to its sex ratio, but understanding the underlying mechanisms will require additional efforts.

Résumé : Les tendances démographiques à long terme s'expliquent généralement par des facteurs extrinsèques à la population, tels que le climat ou la prédation, plutôt que par des facteurs intrinsèques, comme la génétique ou les effets maternels. Nous avons tenté de comprendre la dynamique de population à long terme d'un poisson proie indigène d'importance au lac Michigan, le cisco de fumage, *Coregonus hoyi*. Dans une série chronologique de 38 ans, il s'est produit trois phases de 10–15 ans, de recrutement faible, excellent et de nouveau faible, sans grande variation entre les années durant une phase donnée. Des modèles dynamiques linéaires nous ont servi à déterminer si la variation du recrutement s'explique par des facteurs extrinsèques (températures de l'hiver et du printemps, densité des prédateurs) ou intrinsèques (production d'oeufs de la population, condition des adultes, sex-ratio des adultes). Les modèles qui incluent la production d'oeufs de la population, le sex-ratio, les températures d'hiver et de printemps et la condition des ciscos adultes expliquent le maximum de variation. De ces variables, le sex-ratio, qui va de 47 à 97 % dans la série chronologique, a régulièrement l'effet le plus prononcé : le recrutement diminue lorsque les femelles prédominent. L'addition de la biomasse des prédateurs, les gaspareaux adultes, dans le modèle n'explique pas de variation supplémentaire. Dans leur ensemble, nos résultats indiquent que le recrutement du cisco de fumage est relié au sex-ratio, mais il faudra faire des travaux additionnels pour comprendre les mécanismes sous-jacents.

[Traduit par la Rédaction]

Introduction

Ecologists have long sought to understand the dynamics of populations within a time series. Some dynamics are more short term, with stochastic fluctuations from year to year. Others are more long term, and some can even be characterized by predictable oscillations or cycles. To explain both types of trends, ecologists have focused on the role of factors both extrinsic (e.g., abiotic factors, predation, interspecific competition, disease) and intrinsic (e.g., cannibalism, genetics, maternal effects) to the population. Extrinsic factors, however, have generally received greater attention when trying to explain long-term changes in population abundance. For example, decadal fluctuations in porcupine abundance relate to 11- and 22-year cycles in solar activity (Klvana et al. 2004), and the well-known 10-year cycles of snowshoe hares appear to be regulated by both the abundance of their prey and the densities of their predator, the lynx (Krebs et al. 2001). Evidence for factors intrinsic to the population influencing long-term trends has generally been limited to ma-

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ternal effects on reproductive output (e.g., Boonstra 1994; Ginzberg and Taneyhill 1994) or cannibalism or intraspecific competition among cohorts (Bjørnstad et al. 1999; Sanderson et al. 1999).

Ecologists studying fish populations have generally focused on year-to-year fluctuations in abundance rather than on long-term patterns and cycles in abundance. This bias is not a result of fish populations failing to exhibit long-term or cyclical trends. In fact, a meta-analysis of animal populations revealed mammals and marine and anadromous fishes to be the most common taxa to cycle (Kendall et al. 1998). Rather, focus on interannual fluctuations is more likely a result of fish populations commonly producing highly variable and unpredictable numbers of recruits. Because these fluctuations can have a considerable impact on commercial fisheries or on the dynamics within an ecosystem, understanding the mechanisms underlying interannual variation in recruitment has been a primary goal in fisheries (Houde 1987). Recently, however, attention is turning toward longer-term and cyclic trends in the recruitment and population dynamics of exploited anadromous and marine fishes. For example, researchers have found that regional climate patterns (i.e., Pacific Decadal Oscillation, Aleutian Low Pressure index) appear to influence the decadal and multidecadal population trends in Pacific salmon (Beamish and Bouillon 1993), Pacific halibut (Clark and Hare 2002), and Japanese sardine (Wada and Jacobson 1998). Long-term trends of Atlantic cod (*Gadus morhua*) populations off the Norwegian coast, conversely, appear to be influenced by cannibalism and competition among cohorts (Bjørnstad et al. 1999), factors intrinsic to the population.

In this paper, we seek to add to the understanding of long-term population trends of fishes by focusing on a freshwater taxon, the bloater (*Coregonus hoyi*), which exhibits a rather unusual recruitment (i.e., number surviving to age 3) and population trend. Over a 38-year time series in Lake Michigan, bloaters have gone from a phase of low recruitment (1964 to 1976) and low population size to a phase of increased recruitment (1977 to 1994) and population size, and then back to a phase of low recruitment (1995 to 2001) and reduced population size (Madenjian et al. 2002; TeWinkel et al. 2002). Thus, unlike other fishes that typically show strong interannual variability in recruitment over a 10- to 15-year period (e.g., Bjørnstad et al. 1999), bloaters appear to go through regular 10- to 15-year phases of either low or high recruitment (or subsequently low or high population size) without high interannual variation within a phase. Because of the regularity of these phases over 38 years of data, bloater populations have been hypothesized to undergo cycles in abundance (Madenjian et al. 2002), although additional data are needed to verify this hypothesis.

Factors both extrinsic and intrinsic to the population have been hypothesized to influence bloater recruitment in Lake Michigan. Exotic adult alewives (*Alosa pseudoharengus*) have been hypothesized to reduce bloater recruitment by preying on bloater larvae or reducing prey for zooplanktivorous bloater larvae (Wells and McLain 1973; Eck and Wells 1987). Similarly, cold temperatures during winter and spring have been hypothesized to reduce bloater recruitment by lengthening the period of egg development and reducing the growth rates of bloater larvae, which in turn increases susceptibility to predators (Rice et al. 1987). With regard to intrinsic factors, female predominance among adults has been hypothesized to limit recruitment and regulate bloater population size (Brown et al. 1987). For other species such as Atlantic cod, recent studies have found maternal condition to influence the fecundity (Kjesbu et al. 1991), egg quality (Ouellet et al. 2001), and even recruitment to age 3 (Marshall et al. 1999). Because bloaters have exhibited density-dependent growth rates and one of their primary adult prey items, *Diporeia*, has precipitously declined in Lake Michigan (Nalepa et al. 1998), we may expect that changes in bloater condition could influence bloater recruitment. Finally, an underlying theory of fisheries biology is that recruitment is related to some measure of its stock size, such as population egg production (Hilborn and Walters 1992). Using a Bayesian approach to time series analysis, we investigated whether variation in bloater recruitment in Lake Michigan could be explained by these factors extrinsic (adult alewife biomass, winter and spring temperatures) or intrinsic (population egg production, adult sex ratio, adult condition) to the population.

Materials and methods

Bloater commercial fishing and life history in Lake Michigan

Bloaters are the smallest of the seven deepwater cisco species that were once found in the Laurentian Great Lakes (Smith 1964). The larger cisco species were largely extirpated from the lake by the mid-1960s, owing primarily to high rates of commercial harvest (Wells and McLain 1973). By default of the loss of the other ciscoes, bloaters became the target of the commercial fishery by the early 1960s. To estimate the impact of commercial fishing on bloater population dynamics, we calculated exploitation fraction (i.e., biomass of commercial harvest / biomass of population) from 1962 through 2004. Commercial harvest data were made available through the Great Lakes Commercial Catch Database (S.R. Nelson, US Geological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor, MI 48105, USA, personal communication). We extrapolated depth-specific mean densities from our bottom trawl survey (details below) to the area of Lake Michigan between 5 m and 114 m to estimate adult bloater biomass (Madenjian et al. 2005*a*); this is a very conservative population biomass estimate because it assumes an unrealistic catchability coefficient of 1.0 and does not include bloater biomass that occurs in depths 115 m and greater. From 1962 through 1977, these putatively high exploitation fractions averaged 0.23, with an unusually high value of 0.75 in 1974 (Fig. 1). By 1964, commercial fisheries were dominated by gillnets, rather than bottom trawls, and the gillnets used large meshes (>6.4 cm) that targeted larger, older individuals, with age-4 and older bloaters comprising 92%–95% of the catch by number (Brown et al. 1985). Owing to declining bloater population sizes, a commercial fishery closure was enacted in 1976 (Brown et al. 1985). It is unclear when the closure was lifted, but the commercial harvest increased to more than nominal levels (i.e., >600 tonnes) by 1979. Since 1979, however, exploitation fractions have been less than 0.02, on average (Fig. 1). During the early 1970s, however, it is likely

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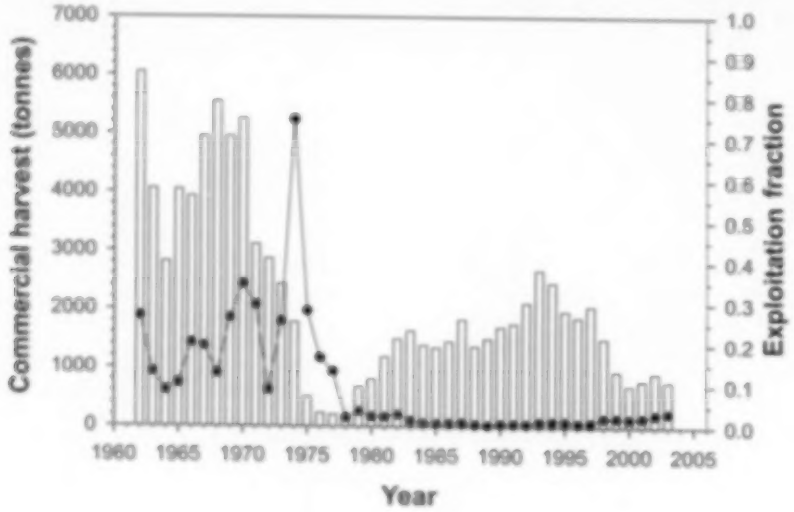
Fig. 1. Time series of commercial harvest (open bars) and exploitation fraction (line graph) of blueters (*Coregonus hoyi*) in Lake Michigan.



that the commercial fishery was reducing the blueter spawning stock biomass and resultant egg production. However, we did not include exploitation fraction as a potential explanatory extrinsic variable in our analyses to explain recruitment for two reasons. First, the commercial fishery was not harvesting age-3 blueters, which was our index of blueter recruitment. Second, the effects of exploitation fraction were already reflected in population egg production, which was included in our analyses.

In Lake Michigan, blueters spawn between January and March on bottom substrate in 40 m to more than 110 m of water (Wells 1966; Emery and Brown 1978; Rice et al. 1987). Newly hatched larvae (i.e., still containing yolk sacs) have been collected in this same habitat during mid-April through mid-August, with the peak densities observed during May and June (Rice et al. 1987). During June through September, larger, older larvae begin migrating to shallower waters and have been sampled near the surface during the day at the same depth contours (Crowder and Crawford 1984; Rice et al. 1987). Age-0 blueters are zooplanktivorous and appear to be daytime feeders (Crowder and Crawford 1984). Blueters continue to occupy the epilimnion and metalimnion through age 1 or even age 2 (Crowder and Crawford 1984). As blueters age (>age 2) and grow to larger sizes (i.e., >150 mm total length, TL), they become benthic and occupy the hypolimnion for the remainder of their life (Crowder and Crawford 1984; TeWinkel and Fleischer 1999). They are concentrated at depths greater than 70 m and remain on the bottom during the day and vertically migrate about halfway through the hypolimnion at night (TeWinkel and Fleischer 1999). Blueters primarily consume amphipods (i.e., *Diporeia* spp.) and opossum shrimp (*Mysis relicta*) but will also consume zooplankton (Crowder and Crawford 1984; TeWinkel and Fleischer 1999). The natural predators of blueters, lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*), also underwent a marked decline by the 1950s as a result of sea lamprey parasitism. Since then, Pacific salmonids have been introduced and lake trout are sustained only through stocking, but these potential predators have generally made blueters only a minor proportion of their diet (Jude et al. 1987; Madenjian et al. 1998).

Field sampling

Since 1962, the Great Lakes Science Center (GLSC) has conducted an annual bottom-trawl survey for preyfish on Lake Michigan (Madenjian et al. 2005*b*). Beginning in 1991, the survey was initiated about 3 weeks earlier than previously so that a GLSC lake trout spawning survey could be completed during late October and early November. The average duration of the survey has been 26 days. Minor changes in the ports and depths that are sampled have occurred over the years. In this paper, we use data from seven ports (Frankfort, Ludington, Manistique, Port Washington, Saugatuck, Sturgeon Bay, and Waukegan) that have been sampled with near consistency since 1973 (Fig. 2). Exceptions include Port Washington in 1976 and 2000, Manistique in 1995, 2000, 2001, and 2002, Saugatuck in 2000, and Waukegan in 2000. In 1998, all ports were sampled but we do not use density data from that year because the trawl was towed at an unusually fast speed (4.7 km·h^{-1}), which affected the catchability. Only one of these ports, Saugatuck, was sampled annually between 1962 and 1972. At each port, a transect of on-contour (i.e., constant depth) fixed sites was fished at up to 11 different depth strata, ranging between 9 m and 110 m with approximately 9-m increments. Because of bottom topography, not all depths could be sampled at all ports. In addition, some depths in some years were skipped for a variety of reasons (i.e., weather, daylight, boat functionality).

Since 1962, GLSC has fished a ¾ Yankee Standard No. 35 bottom trawl (12-m headrope, 15.5-m footrope, and a 13-mm mesh in the cod end) and most tows are generally 10 min in duration. Towing speed averages around 3.4 km·h^{-1}. When the entire catch was less than about 20 kg, fish were sorted

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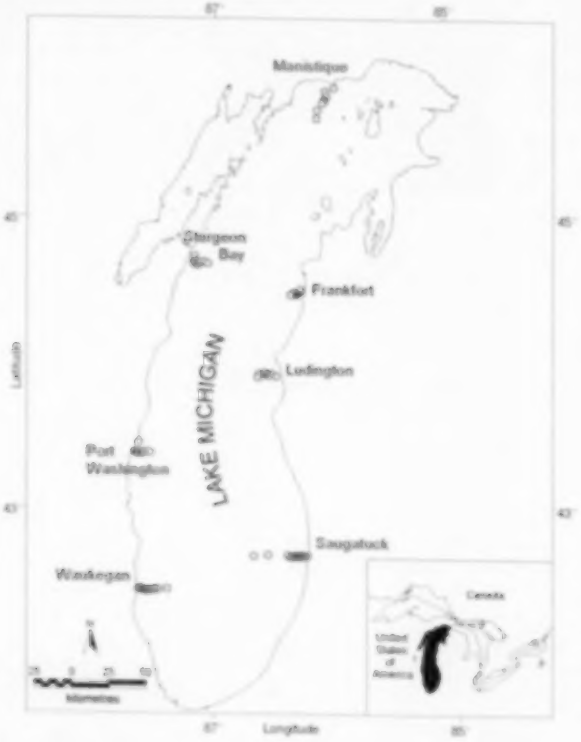
Fig. 2. Map of ports sampled during the US Geological Survey Great Lakes Science Center annual bottom-trawl prey fish survey on Lake Michigan (the inset shows the location within the Great Lakes region). Each circle identifies a fixed depth station that is sampled within a particular port.



by species and counted, and an aggregate species weight was measured. In larger catches, a random sample of 10–15 kg was selected for species sorting and counting and aggregate weighing. The remainder of the catch was then weighed for later extrapolation of the sorted sample. The TL of up to 100 randomly encountered bloaters from the sorted sample were measured to the nearest millimetre.

Bloaters captured from four ports (Frankfort, Manistique, Saugatuck, and Waukegan) were stored on ice for no more than 24 h so that subsequent processing would provide length, weight (nearest gram), sex, and maturity information, as well as scale collections. Through 1982, these fish were randomly selected at each port. After 1982, however, the first 10 fish encountered from each 10-mm length class at each port were selected. Visual inspection of the gonads revealed the sex and whether bloaters were mature or immature. In the laboratory, ages were determined by counting the number of annuli on a projected scale image. Bloater ages ranged from 0 to 13 years.

Generating time series estimates

Abundance of age-3 recruits

Bloaters do not fully recruit to our bottom trawl until age 3, which corresponds to the age at which bloaters are believed to have fully transitioned to the benthic habitat from the pelagic. For each trawl, we calculated the number of bloaters in each age class for each sex by constructing age–length and sex–length keys. To do this, we applied the keys to the length distribution of the catch and then expanded the resultant age and sex distributions to the total catch density of the trawl. Before 1998, bloaters were categorized into two stages, roughly age 0 and age 1 and older, and catch densities and length frequencies were recorded for each stage in each trawl. For 139 of 3227 combinations of year, port, depth, and stage (i.e., 4% of combinations), length frequencies were not available. When this occurred, we first sought to substitute with the average length frequency from the same stage, depth, and year of the other ports. We looked to similar depths because depth (age 0, $F_{[10,9601]} = 89.4$; age 1 and older, $F_{[10,55524]} = 932.1$) explained more of the variation in bloater size for a particular stage than port (age 0, $F_{[6,9601]} = 72.0$; age 1 and older, $F_{[6,55524]} = 372.6$) or year (age 0, $F_{[6,9601]} = 58.1$; age 1 and older, $F_{[29,55524]} = 449.8$) in a general linear model. Where similar depths from the same stage and year were unavailable, we used the average length frequency from adjacent depths at the same port of that year as a second option or from adjacent depths of other ports of that year as a third option. As a last option, we used the average length distribution from the same depth of all ports in adjacent years.

We constructed year-specific sex–length keys by pooling all bloaters of known sex and then calculating the proportion by sex for each 10-mm length class. However, we had insufficient sample sizes (i.e., ≤5 fish) to calculate the proportion of sexes for smaller (i.e., <180 mm TL) and larger (>290 mm TL) fishes. For example, in the 140-mm length bin, we had sufficient sample sizes for only 20 of the years between 1962 and 2004. In the year and length bin combination for which we had sufficient sample sizes, however, χ^2 tests rarely found proportions different from 1:1 (1 of 15 years in 120-mm bin; 0 of 17 years in 130-mm bin; 2 of 20 years in 140-mm bin; 1 of 24 years in 150-mm bin; 5 of 25 years in 160-mm bin; 2 of 30 in 170-mm bin). Hence, we assumed equal sex proportions in all length bins less than 180. When sample sizes were insufficient to calculate proportions by sex in length bins 290 mm and larger (occurred in only 13 out of 495 year and length-class combinations), we substituted the proportions from adjacent years.

Age–length keys also were constructed for each year by pooling all aged fish. Previous analysis of GLSC data by Krause (1999), however, suggested that one age–length key per year should be constructed for all southern ports and another for all northern ports because of differences in size at age between the ports in 1973–1993. We conducted a similar analysis with all 39 years of available aging data: we used a general linear model with age as the response variable and fish size, port, year, and interactions between fish size and port and fish size and year as explanatory variables. All explanatory variables except port exhibited a strongly significant effect on age (i.e., $P < 0.01$). The effect of port, however, was only marginally significant (i.e., $P = 0.06$). Bonferroni multiple comparisons of least-squares mean age at various bloater sizes revealed no latitudinal pattern in port groupings, as Krause (1999) had found. Manistique and

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Saugatuck, which occur at northern and southern ends of the lake, respectively, generally exhibited small sizes at age. Sturgeon Bay and Port Washington, which are more centrally located on the western shore, generally exhibited large sizes at age. The remainder of the ports grouped with either the smaller or larger sizes at age, depending on the size at which the least-squares mean was calculated. Hence, without clear groupings of ports emerging across the lake, we decided to pool all age data to make one age–length key per year.

Even with only one age–length key per year, we still had to fill in age proportions when aging data were unavailable for some length bins. This occurred in only 3.5% of the year and bloater 10-mm length bin combinations and was limited to bins less than 180 mm and greater than 280 mm. To substitute missing values, we averaged the age proportions in the same 10-mm length bin of adjacent years. During the 1960s, however, bloaters were not aged in 1962–1964 and 1966. For all these years, we used the same age–length key, which was the average of all available annual age–length keys between 1965 and 1977, when bloaters were at a relatively low abundance (and density-dependent effects on size at age should have been minimized).

After applying the keys to the length distribution, we then used the catch density (number·ha^{-1}) to estimate the density of bloaters by age class and sex. The area swept was corrected for trawl width (in metres, = 9.693 – (43.93/depth)) and time on bottom (in minutes, = tow time – 3.875 + depth$^{0.412}$) as a function of depth (m), based on trawl mensuration results. Because we were interested in the abundance of age-3 recruits, we calculated the average density of age-3 recruits at each of the 11 depth strata and then multiplied the mean density by the area of the lake represented by its depth strata. We then summed the density of recruits across the 11 depth strata to represent the abundance of age-3 recruits. We note that our abundance estimate is not truly lake-wide because our summation includes only depths between 5 m and 114 m, which represent about 67% of the entire lake.

To estimate age-3 bloater abundance between 1962 and 1972, we have data for only one port, Saugatuck, and only seven depth strata were consistently measured over that time period. To make these data more comparable with years 1973 and later, when all seven ports and all 11 depth strata were available, we calculated a conversion factor (sensu Madenjian et al. 2005*b*). Using data from 1973–2004, we divided the lake-wide abundance estimates based on mean densities using all ports and depth strata by the lake-wide abundance estimate based on densities using only Saugatuck and its seven depth strata that were available before 1973. These annual ratios were lognormally distributed, ranging from 0.45 to 14.6. The mean of this lognormal distribution equaled 2.38. For the years 1962–1972, we then multiplied the Saugatuck lake-wide abundance estimate by the 2.38 conversion factor.

Population egg production

To calculate population egg production, we used the aforementioned length distributions, age–length and sex–length keys. In addition, we constructed an annual maturity key that was a function of bloater sex and size (10-mm length bin). As in the sex–length key, when proportional maturity data were unavailable for a particular size in a given sex and year, data from adjacent years with the same size and sex of the bloater were substituted. With these keys, we could estimate the density of mature females in each 10-mm length bin in each depth and port and then calculate the mean density at each depth across ports. We then extrapolated the number of mature females in each 10-mm length bin in the 5- to 114-m depth strata (as with the abundance of age-3 recruits). Because bloater total fecundity is best predicted by bloater weight in grams (fecundity = 580.6 + 58.88(weight); Emery and Brown 1978), we then calculated an annual length–weight regression to convert each 10-mm length bin to a weight and then calculate the number of eggs that would be produced. We assumed that our autumn bottom trawl survey would provide an estimate of the population egg production for the following year. To calculate population egg production between 1962 and 1972, we used the same methods as with age-3 bloater abundance to calculate a conversion factor of 2.40.

Condition and sex ratio of adult bloaters

We used Fulton's condition index (K) as a measure of adult bloater condition. Our estimates of annual mean K are highly correlated ($r = 0.87$, $P < 0.0001$) with mean percent lipid content in 14 years for which lipid data are available (Hesselberg et al. 1990; Madenjian et al. 2000). For years 1967 and later, we calculated the annual mean K of all age-2 and older bloaters, where K = (weight·length^{-3}) × 100 000. For years prior to 1967, so few fish were aged that we included bloaters greater than 165 mm TL in our calculation of annual mean K. As with population egg production, we used the condition of bloaters in our fall survey to represent the condition of the adults that would produce the year class for the following year.

To represent adult sex ratio, we calculated the percentage of adults that were female. For the years 1966 through 2004, we considered adults to be those bloaters age 2 and older. On average, this percentage was calculated using 439 bloaters (range 97–1145). For the years before 1967 when few bloaters were aged, we considered adults to be larger than 165 mm TL. On average, this percentage was calculated using 250 bloaters (range 57–517).

Adult alewife biomass and winter–spring temperatures

For a time series of adult alewife biomass, we used the same time series from Madenjian et al. (2005*b*), which was based on the same GLSC data that we used. To construct a time series of winter and spring temperatures, we used a model of evaporation and thermodynamic fluxes developed for Lake Michigan by the Great Lakes Environmental Research Laboratory (Croley 1995). The model uses daily inputs of air temperature, wind speed, humidity, and cloud cover at six locations around the lake and was calibrated using surface water temperatures and ice cover concentrations during 1991–1995. The model generates a daily profile of water temperatures at 1-m depth increments from the surface to the bottom of the lake (282 m). We used habitat data of age-0 bloaters (see Bloater life history in Lake Michigan above) to select the 40- to 100-m depth strata for use as an index of winter–spring temperatures. We calculated a daily integrated temperature for that depth layer and subtracted 4

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from each daily temperature value so that colder values were smaller (or more negative). The annual winter–spring temperature index equaled the sum of the daily values between 1 January and 30 June of each year.

Time series analysis

We used dynamic linear models (DLMs) to determine how the time series of bloater recruitment to age 3 related to the time series of population egg production, population sex ratio, adult condition, adult alewife biomass, and winter and spring temperatures. DLMs have been used successfully in many different ecological time series to detect trends and identify important explanatory variables (e.g., Lamon et al. 1998; Scheuerell et al. 2002; Schindler et al. 2005). Initially, however, we had attempted to fit our data to a Ricker stock–recruit model that included external variables (Hilborn and Walters 1992). A nonstationary pattern in the stock–recruit time series was apparent, however (Fig. 3). For a given level of population egg production, there was a much higher level of recruitment in the 1980s than in the early 2000s, making a "loop" in the time series (sensu Walters 1987). Using a DLM, we acknowledged that the sequence of the data was providing critical information in that the response in one year was strongly related to the response one year earlier.

DLMs are Bayesian time series models (for a full description, see Pole et al. (1994)). Because Lamon et al. (1998) and Scheuerell et al. (2002) provide detailed explanations for ecological applications of DLMs, we will only briefly describe our methods here. Each DLM uses two time-dependent (t) equations, referred to as observation and systems equations. In the observation equation, the response variables (Y_t) are sequentially fitted to a $1 \times m$ vector of predictor variables ($\mathbf{X}_t$) with a $m \times 1$ vector of model parameters ($\boldsymbol{\theta}_t$) and a normally distributed error term (v_t):

$$(1) \qquad Y_t = \mathbf{X}_t\boldsymbol{\theta}_t + v_t, \quad v_t \sim N[0, V_t]$$

In our models, the value of m equaled the number of explanatory regression variables that were included, plus the level and growth parameters associated with a dynamic linear trend. The observation errors had a time-dependent variance (V_t) that was estimated from prior data and used a "discounting" scheme that determines how many years of prior data are used (see below).

The systems equation uses prior information through Bayesian learning to allow the model parameters $\boldsymbol{\theta}_t$ to change with each time step through a first-order Markov process:

$$(2) \qquad \boldsymbol{\theta}_t = \mathbf{G}\boldsymbol{\theta}_{t-1} + \boldsymbol{\omega}_t, \quad \boldsymbol{\omega}_t \sim N[0, \mathbf{W}_t]$$

where $\mathbf{G}$ is the $m \times m$ system evolution matrix that determines how the model parameters change and $\boldsymbol{\omega}_t$ is $m \times 1$ vector that describes the stochastic change in normally distributed parameters through time. The system covariance matrix $\mathbf{W}_t$ describes the variance of the parameters through time, and a discount factor is again applied to determine the amount of prior data used in the estimation at each time step.

The discount factor allows the model to change the importance of recent observations when making predictions of model parameters and variance for the next time step. Theoretically, discount factors can range from 0 (no prior data are considered) to 1 (all prior data are considered), but Pole et al. (1994) recommend setting discount factors to be at least 0.8. In addition, we always set the discount factor for the regression parameters to be greater than that for the trend parameters (i.e., level and growth parameters), but the difference between the two discounts was never greater than 0.1, as recommended by Pole et al. (1994).

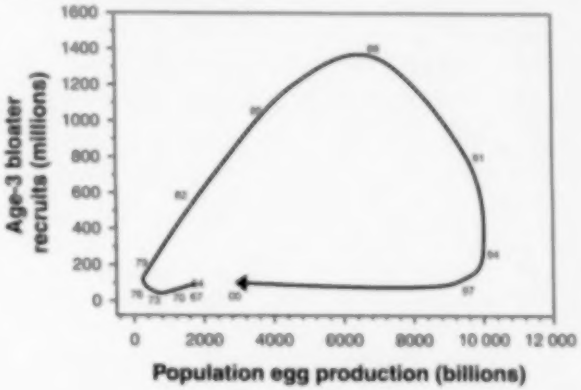

Fig. 3. Stock–recruit relationship for bloater (*Coregonus hoyi*) in Lake Michigan. Each data point represents the average of three consecutive years of data; the numbers represents the last two digits of the median year class for those three years (e.g., "88" represents the average of the 1987–1989 year-classes. The arrow was added to demonstrate the "loop" or nonstationarity in the relationship (see Walters 1987).

Before fitting each model, we (*i*) $\log_e$-transformed the response variables such that they were normalized and (*ii*) standardized (mean deleted and divided by the standard deviation) the explanatory variables to improve the estimation of the level parameter and allow direct comparison of the explanatory variable coefficients (Pole et al. 1994). For each model, we systematically varied the discount factors until the combination that maximized the log-likelihood in the forecast model was identified. Once the discount factors were determined, we then fit the data retrospectively with the appropriate discount factors and used the residuals to calculate the negative log-likelihood (NLL) for that model:

$$(3) \qquad \text{NLL} = n[\log_e(\sigma) + 0.5\log_e(2\pi)] + \text{SSE}/2\sigma^2$$

where n is the number of observations, SSE is the sum of the squared residuals, and σ^2 is SSE divided by n (Hilborn and Mangel 1997). We conducted all of our analyses using the BATS statistical package (Pole et al. 1994). For all models, we evaluated whether serial correlation of the residuals existed, as indicated by a nonrandom pattern in the residuals of the forecast model. Those that were identified to have serial correlation were not considered in the model rankings (see below).

We used two different response variables: the abundance of age-3 recruits (i.e., $\log_e$(recruits)) and reproductive success (i.e., $\log_e$(recruits/population egg production), sensu Wada and Jacobson 1998). When modeling abundance of recruits as the response, we considered 17 different models (each model contained population egg production), and then we considered every possible combination of the four poten-

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tial explanatory variables (bloater sex ratio, adult bloater condition, adult alewife biomass, and winter and spring temperatures). In addition, we included a reference model that contained only the level and growth trend parameters and no explanatory variables. When modeling reproductive success as the response variable, we considered 16 different models. None of the models contained population egg production because it was already considered in the response variable. Within each response variable, we ranked competing models according to the Bayes information criterion (BIC):

$$\text{(4)} \qquad \text{BIC} = 2(\text{NLL}) + m[\log_e(n)]$$

where m is the number of estimated parameters (level, growth, regression parameters) plus the observation variance estimate (v_i), NLL is the negative log-likelihood, and n is the sample size (Box et al. 1991). The model with the smallest BIC was ranked highest, as it provided the most parsimonious fit to the data. To make a pairwise comparison between models i and j, where the $\text{BIC}_i < \text{BIC}_j$, we used the Schwarz criterion (Kass and Raftery 1995):

$$\text{(5)} \qquad S_{ij} = (\text{BIC}_j - \text{BIC}_i)/2$$

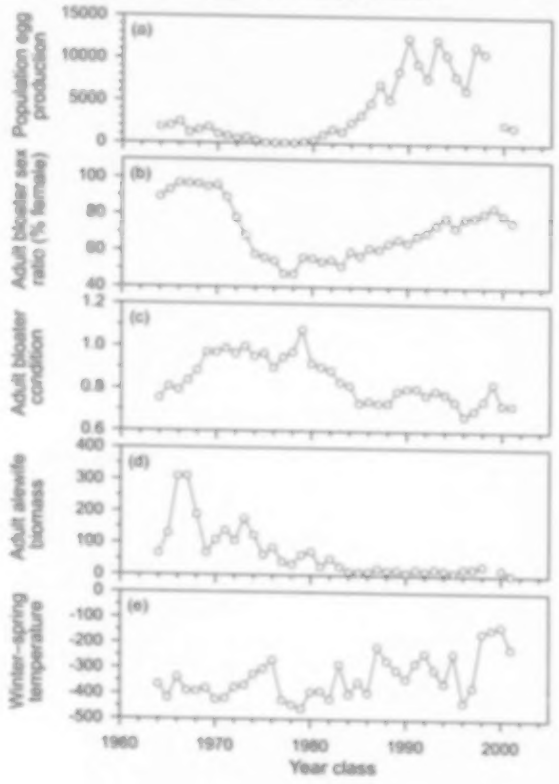
According to Kass and Raftery (1995), when $2S_{ij}$ is between 0 and 2, the evidence for the higher ranked model is "not worth more than a bare mention"; as the difference increases, the evidence for the higher ranked model becomes "positive" (2–6), "strong" (6–10), and even "very strong" (>10).

Results

The explanatory variables demonstrated dynamic trends over the three decades (Fig. 4). Population egg production lagged a few years behind the abundance of age-3 recruits: declining through the 1977 year class, increasing through the 1990 year class, and then fluctuating before declining in the final years (Fig. 4*a*). The sex ratio of the population was nearly always skewed toward females (Fig. 4*b*). In the 1960s, more than 85% of adults were females, but that percentage gradually declined to reach 47% for the 1977 year class. As recruitment increased, however, the sex ratio steadily increased through the 1999 year class, attaining levels of more than 80% female. Condition of adults increased early in the time series until generally stabilizing through the 1970s (Fig. 4*c*). During the 1980s through the mid-1990s, condition declined as the bloater population increased in size, because of strong recruitment. Condition increased slightly in the final years of the time series but did not reach levels as high as in the early 1970s. Biomass of adult alewife peaked in the late 1960s, declined through the early 1980s, and has remained consistently low since then (Fig. 4*d*). Finally, winter and spring temperatures have fluctuated considerably, but the overall trend appears to suggest warmer years in the latter half of the time series (Fig. 4*e*).

The time series of the two response variables were somewhat similar in that both declined through the 1960s, then increased, and subsequently declined again (Figs. 5*a*, 6*a*). Age-3 recruits increased through the 1989 year class before stabilizing and declining, whereas reproductive success increased through only the 1978 year class and then declined.

Fig. 4. Time series of the explanatory variables (raw values) that were used in the dynamic linear models: (*a*) population egg production, in billions of eggs; (*b*) adult bloater (*Coregonus hoyi*) sex ratio; (*c*) Fulton's condition factor of adult bloaters; (*d*) biomass of adult alewife (*Alosa pseudoharengus*), in kilotonnes; and (*e*) index of winter and spring temperatures (1 January through 30 June) between depths of 40 m and 100 m in Lake Michigan (more negative values equals colder temperatures).



Reproductive success increased slightly in the final years of the time series, whereas the abundance of age-3 recruits did not.

When abundance of age-3 recruits was the response variable, the top-ranked model included population egg production, sex ratio, bloater condition, and winter and spring temperatures (i.e., every explanatory variable except alewife; Table 1). The retrospectively fit model explained nearly all of the variation in the observed data (Fig. 5*a*; the coefficient of determination, r^2, from plot of predicted versus observed, equaled 0.999). As expected, the coefficient for population egg production was positive throughout the time series, but the high value of the coefficient through the 1960s and 1970s indicates that population egg production had its greatest effect during this time period (Fig. 5*b*). Among the other explanatory variables, sex ratio had the greatest impact during the time series with its 90% credible intervals different from zero for the majority of the time series (Fig. 5*c*). Overall, sex ratio was inversely associated with recruitment (i.e., stronger recruitment occurred when sex ratios were more balanced).

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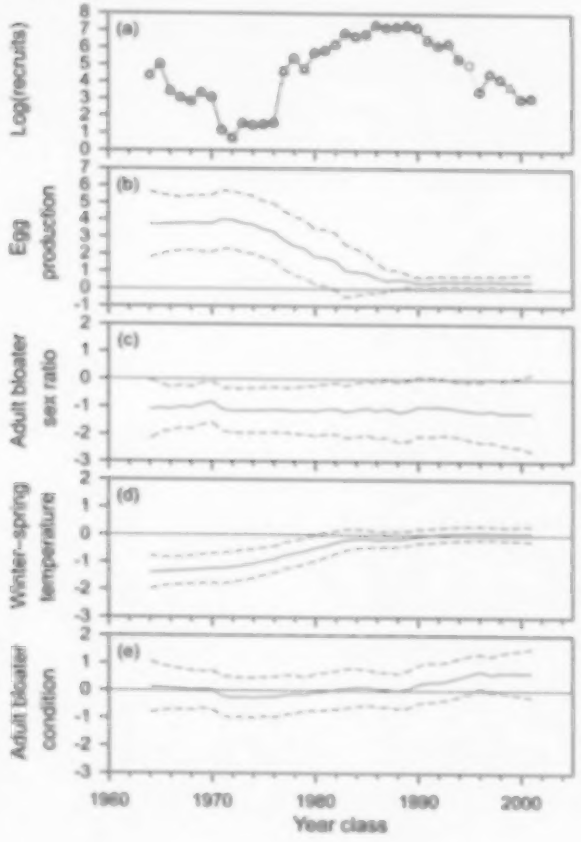
Fig. 5. Time series results of the top-ranked dynamic linear model when the abundance of age-3 bloater (*Coregonus hoyi*) recruits was the dependent variable. (*a*) The observed (open triangles) and model-predicted (open circles) abundance ($\log_e$-transformed) of age-3 recruits. (*b*–*e*) The coefficient (solid line) and 90% Bayesian credible intervals (broken lines) for explanatory variables population egg production, adult bloater sex ratio, winter and spring temperatures, and adult bloater condition, respectively. Note that the *y* axes are equal in *c*–*e* and are unique in *a* and *b*.



Winter and spring temperatures also were inversely associated with recruitment until the early 1980s when the coefficient began hovering around 0 (Fig. 5*d*). Opposite from the Rice et al. (1987) hypothesis, recruitment was higher during years of colder temperatures relative to warmer ones. Finally, adult bloater condition appeared to have the least impact on recruitment as its 90% credible intervals were not different from zero for nearly the entire time series (Fig. 5*e*). Late in the time series, adult condition was positively related to recruitment, as we had hypothesized. The second-ranked model included all variables of the top-ranked model except bloater condition, but the Schwarz criterion revealed a difference of 18, indicating very strong evidence for the top-ranked model over the second-ranked one. Compared with the reference model with no explanatory variables, however, the Schwarz criterion found very strong evidence that all models provided better support. Only three of the models, each ranked far below the top-ranked model, exhibited serial autocorrelation in the forecast residuals (Table 1).

Table 1. Summary of dynamic linear models to explain variation in abundance of age-3 bloater (*Coregonus hoyi*) recruits in Lake Michigan over the 1964–2001 year classes.

Explanatory regressor variable(s)	*m*	NLL	BIC
EGG, SEX, WIN, CON	7	−144.5	−264.0
EGG, SEX, WIN	6	−133.8	−246.1
EGG, WIN, ALE, CON	7	−125.0	−224.9
EGG, SEX, WIN, ALE, CON	8	−119.6	−210.5
EGG, WIN, CON	6	−114.5	−207.5
EGG, SEX, CON	6	−101.0	−180.5
EGG, SEX, WIN, ALE	7	−88.4	−151.7
EGG, SEX, ALE, CON	7	−77.4	−129.7[a]
EGG, ALE, CON	6	−70.6	−119.6
EGG, WIN, ALE	6	−68.4	−115.3
EGG, CON	5	−55.3	−92.6
EGG, ALE	5	−36.7	−55.4[a]
EGG, WIN	5	−34.8	−51.6
EGG, SEX, ALE	6	−34.6	−47.6[a]
EGG, SEX	5	−27.3	−36.6
EGG	4	−19.6	−24.9
	4	17.0	48.4

Note: Codes for explanatory regressor variables: EGG, population egg production; SEX, adult bloater sex ratio; CON, adult bloater condition; WIN, winter temperatures; ALE, adult alewife biomass. All models also included the level and trend parameter estimates. *m*, number of parameters; NLL, negative log-likelihood; BIC, Bayes information criterion.
[a]Serial autocorrelation in the residuals was identified.

When reproductive success was the response variable, the top-ranked model included every explanatory variable: sex ratio, bloater condition, winter and spring temperatures, and alewife (Table 2). The second-ranked model included all of the explanatory variables of the top-ranked model except alewife. The Schwarz criterion revealed a difference of 5.9 between the top two models, offering positive evidence for the top-ranked model over the second-ranked one. Although there was BIC evidence to favor the top-ranked model, we chose the second-ranked model as the best model because the 90% credible intervals for the alewife coefficient were never different from zero in the top-ranked model. The retrospectively fit model explained nearly all of the variation in the observed data (Fig. 6*a*; r^2 from plot of predicted versus observed equaled 0.999). The trends in coefficients were very similar to the trends of coefficients for the top-ranked model when abundance of age-3 recruits was the response variable. The coefficient for sex ratio was always negative (Fig. 6*b*) and was most strongly inversely associated with reproductive success during the late 1970s and early 1980s. Winter and spring temperatures were inversely associated with reproductive success in the late 1960s and early 1970s (Fig. 6*c*); later in the time series, its effects were minimal. Finally, adult bloater condition (Fig. 6*d*) was positively related to reproductive success early (1960s) and late (late 1990s) in the time series; during the other periods, the effects of adult bloater condition were minimal. Using the Schwarz criterion, all 15 models with explanatory variables provided were found to have very strong support for a better

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Table 2. Summary of dynamic linear models to explain variation in reproductive success (abundance of age-3 bloater (*Coregonus hoyi*) recruits divided by population egg production) in Lake Michigan over the 1964–2001 year classes.

Explanatory regressor variable(s)	*m*	NLL	BIC
SEX, WIN, ALE, CON	7	−131.4	−237.7
SEX, WIN, CON	6	−126.6	−231.8
SEX, WIN	5	−112.3	−206.6
SEX, WIN, ALE	6	−102.2	−182.9
SEX, CON	5	−99.6	−181.3
SEX, ALE, CON	6	−99.9	−178.2
WIN, CON	5	−91.1	−164.3
WIN, ALE, CON	6	−83.8	−146.1[a]
SEX, ALE	5	−70.6	−123.3
ALE, CON	5	−40.8	−63.7
CON	4	−29.6	−44.8
SEX	4	−22.0	−29.8
WIN, ALE	5	−5.8	6.4
WIN	4	0.4	15.2
ALE	4	10.0	34.4[a]
	3	26.9	64.6

Note: Codes for explanatory regressor variables: SEX, adult bloater sex ratio; CON, adult bloater condition; WIN, winter temperatures; ALE, adult alewife biomass. All models also included the level and trend parameter estimates. *m*, number of parameters; NLL, negative log-likelihood; BIC, Bayes information criterion.

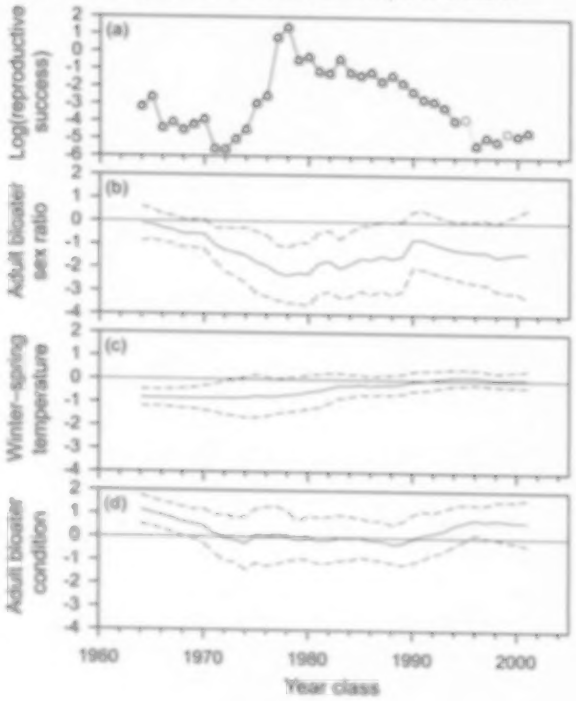
[a]Serial autocorrelation in the residuals was identified.

fit to the data than the reference model without any explanatory variables. Only two of the models, each ranked far below the top-ranked models, exhibited serial autocorrelation in the forecast residuals (Table 2).

Discussion

In the 1964 through 2001 year classes, bloater recruitment and bloater reproductive success (abundance of recruits divided by population egg production) followed a fairly smooth trend without the high interannual variability typically observed in fish species. Recruitment went through three phases: declining from the early 1960s through the early 1970s, increasing through the late 1980s, and then declining again through the early 2000s. Because each phase occurred over intervals of 15 years or so, our 38-year time series is insufficient to document regular bloater recruitment (and adult population abundance) cycling; additional years of GLSC surveys will determine whether bloaters undergo regular cycles (as proposed by Madenjian et al. 2002). Our objective was to use Bayesian time series analyses to determine whether the variation in bloater recruitment and reproductive success was explained by factors extrinsic or intrinsic to the population. Unlike most studies that have explained long-term trends with extrinsic factors, our analyses revealed that adult sex ratio, an intrinsic factor, explained more variation in recruitment than extrinsic factors. Another intrinsic factor, an index of adult bloater physiological condition, explained some of the variation early and late in the time series. With regards to extrinsic factors, biomass of adult alewives failed to explain variation in the time series, and winter and spring temperatures during the period of bloater

Fig. 6. Time series results of the second-ranked dynamic linear model when reproductive success ($\log_e$(recruits/population egg production)) was the dependent variable. We considered this model superior to the top-ranked model for two reasons: (*i*) the top-ranked model included an additional variable (adult alewife biomass) for which the 90% Bayesian credible intervals were never above or below the zero line; and (*ii*) the difference in BIC (Bayes information criterion) between the top-ranked models was minimal. (*a*) The observed (open triangles) and model-predicted (open circles) abundance ($\log_e$-transformed) of reproductive success. (*b*–*d*) The coefficient (solid line) and 90% Bayesian credible intervals (broken lines) for explanatory variables adult bloater (*Coregonus hoyi*) sex ratio, winter and spring temperatures, and adult bloater condition, respectively. Note that the *y* axes are equal in *c* and *d* and are unique in *a* and *b*.



egg and larval development explained some of the variation, but only early in the time series.

The most important explanatory variable throughout the time series, adult sex ratio, demonstrated a smooth trend of declining and then increasing female predominance across the Lake Michigan time series. Bloater female predominance is caused primarily by higher longevity among females than males (TeWinkel et al. 2002), as initial sex ratios are roughly equal. Among age-2 bloaters, the earliest age for which we have reliable data, 53% (average of annual percentages, range = 35–78%) are females since 1973. Although this average percentage is greater than 50% ($t_{30} = 2.41$, $P = 0.02$), it is not sufficient to explain the increasing percentage of females among older age classes (e.g., 73% for age 5, 81% for age 7, 91% for age 9). Additional evidence that initial sex ratios are not biased comes from a laboratory study that found equal sex ratios at hatching across a range of tempera-

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tures (Eck and Allen 1995), indicating that abiotic factors do not influence sex ratio as found for some other animals (Charnov and Bull 1977).

Why males die sooner than females is unclear. In Lake Michigan, male bloater condition, measured as Fulton's condition factor, is slightly lower than female bloater condition for a given age (paired t tests: age 2, $t_{36} = -1.92$, $P = 0.03$; age 3, $t_{37} = -2.88$, $P = 0.003$; age 4, $t_{37} = -7.36$, $P < 0.0001$), suggesting that males are at an energetic disadvantage that could make them more susceptible to natural mortality than females. One potential explanation for low male condition or high male natural mortality is that males mature slightly earlier than females, but the difference is generally not greater than 1 year (TeWinkel et al. 2002; D.B. Bunnell, unpublished data). The energetics associated with building gonads is likely insufficient to explain the differences between sexes because building testes requires little energy relative to ovaries. In other fishes, however, male spawning behavior can require more energy than female spawning behavior (e.g., Jonsson et al. 1991), which could explain differences in their mortality rates. Unfortunately, bloater spawning behavior has not been characterized.

A dynamic bloater sex ratio that includes periods of female predominance is not just a recent phenomenon in Lake Michigan. Using bottom-set gillnets, Jobes (1949) reported a bias towards females in 1930 (69%), 1931 (65%), and 1932 (80%). In 1919, however, males predominated (36% female; Jobes 1949). Female predominance also was observed by Brown (1970) between 1954 and 1955 in both bottom-set gillnets (82%) and bottom trawls (72%) and then again between 1960 and 1961 (90% in bottom trawls, 87% in gillnets). To address concerns that female predominance is an artifact of seasonal changes in bottom distribution among the sexes, Jobes (1949) observed female predominance in May, June, July, August, and September of 1931 and 1932. Additionally, Brown (1970) allayed concerns that females may occupy deeper depths than males by reporting 99% predominance of females in mid-water trawls ($N = 347$ fish) and 97% predominance among bottom trawls ($N = 4348$ fish) in 1967. Bloaters also have exhibited periods of female dominance in Lake Huron (Schaeffer 2004; Dobiesz et al. 2005) and in Lake Ontario (Stone 1944). Finally, other deepwater ciscos also have demonstrated high percentages of females across the Great Lakes basin (see summary by Brown 1970).

Can female predominance mechanistically influence bloater recruitment and population dynamics as our time series analyses have suggested? One potential mechanism is inbreeding caused by too few male parents, which may lead to long-term suppression of population size until outbreeding can resume (Maynard Smith and Stenseth 1978). We know of no genetic evidence of inbreeding within the Lake Michigan bloater population, however. A second potential mechanism is too few males limiting the number of eggs that are actually fertilized during periods of female predominance (Brown et al. 1987). Using GLSC Lake Michigan bloater data through 1984, when the adult population was about 60% female, Brown et al. (1987) predicted that female predominance would continue to rise and bloater recruitment would ultimately decline. Indeed, their predictions were borne out. We are unaware of other studies that have indicated that the number of male fishes can limit recruitment. Even though the statistical link between sex ratio and bloater recruitment is strong, unanswered questions regarding the mechanism by which sex ratio influences recruitment remain. First, during the period of strong recruitment (1977–1994), sex ratio linearly increased from around 47% to 80% female. However, during 1973–1976 when recruitment success (which accounts for differences in population egg production) was relatively low, sex ratio ranged from 54% to 68% female, within the range of sex ratios during the strong recruitment phase. Given the relatively balanced sex ratio during 1973–1976, it is unclear why recruitment success was not higher. Second, the resurgence of bloater recruitment in 1977 coincided with a bloater sex ratio just under 50%. In the early 2000s, females have comprised at least 70% of the adult population. Must the sex ratio decrease to less than 50% female, as it did in 1977, before bloater recruitment will return to a high phase in the coming years? Increased knowledge of bloater reproductive behavior and population model simulations may provide further insight into how bloater sex ratio influences recruitment. Without this understanding, we cannot exclude the possibility that sex ratio simply covaries with the factor that is truly critical to bloater recruitment success.

When recruitment was the response variable, the coefficient for population egg production in the top-ranked model was always positive. The value of the coefficient, however, was up to four times greater during the 1960s and early 1970s than it was during the 1980s and later. The time series of population egg production revealed relatively high levels of production during the mid-1980s through late 1990s compared with earlier years. Taken together, we interpret the lower coefficients during the mid-1980s and later as a consequence of the density-dependent recruitment that likely was occurring when population egg production reached high levels. This is consistent with general stock–recruitment theory (Hilborn and Walters 1992).

Although not explicitly included in our model, the commercial fishery likely influenced intrinsic variables that were included. First, the nadir in population egg production in the mid-1970s was likely enabled by a fishery targeting larger, older (age 4 and older) bloaters with their gillnets (Brown et al. 1985) at a much higher exploitation fraction than occurred in later years (exploitation fraction means: 1962–1977, 0.23; 1978–2003, 0.02). Second, because these larger, older individuals were primarily female, it is also possible that the fishery contributed to the nearly equal sex ratios that occurred during the mid-1970s. Coincidentally or not, the first strong year class in 10 years occurred in 1977, the year after the closure of the commercial fishery (Brown et al. 1985). Over the next 15 or so years, several consecutive strong year classes were produced but exploitation fractions remained at such low levels that the fishery could not have had any direct or indirect role in the poor recruitment levels that were observed in the late 1990s and early 2000s.

Because bloater recruitment began to increase in the late 1970s as alewife densities were reduced, many biologists hypothesized that adult alewives, which are known to prey on pelagic larvae (Krueger et al. 1995), had been suppressing bloater recruitment in the 1960s and early 1970s (Wells and McLain 1973; Eck and Wells 1987). This hypothesis lost support in the late 1990s, however, when bloater recruitment

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worsened in the face of relatively low alewife densities (Madenjian et al. 2002). Our time series analysis further discredited the role of alewife as effectors of bloater recruitment. Models with alewife generally ranked low in terms of explanatory power, and credible intervals around the alewife coefficients were never different from zero. Although alewife may negatively influence other native fish species in the Great Lakes (Madenjian et al. 2002), our analyses suggest that alewives do not negatively influence bloaters.

Many recent studies have found regional climate patterns to explain variation in long-term trends of population abundance (Beamish and Bouillon 1993; Wada and Jacobson 1998; Clark and Hare 2002). Rice et al. (1987) hypothesized that warmer winter and spring temperatures (and subsequently faster egg development and larval growth) would enhance recruitment by reducing the period of vulnerability to egg and larval predators. The Lake Michigan temperature models that we used revealed winter and spring temperatures to have generally warmed, with considerable variation, over the course of our time series. Our dynamic linear models revealed an inverse relationship between temperatures and recruitment during the 1964–1980 year classes: colder temperatures were associated with stronger recruitment. It is possible that this result is a spurious correlation. However, the Rice et al. (1987) hypothesis focused on the period of fertilized egg incubation and larval growth. The critical temperature effect could occur earlier, during the period of gonadal maturation. Temperatures outside of the optimal range for gonadal maturation have been linked to resorption of their eggs (Tanasichuk and Ware 1987; Sandström et al. 1997). In yellow perch, for example, warmer winter temperatures reduce fecundity and egg viability (Jones et al. 1977; Sandström et al. 1997). Although the negative effect of warmer winter temperatures on bloater gonad maturation is untested, it is one possible mechanism that could explain the unexpected temperature effect found in our model.

The final explanatory variable that we evaluated was adult condition, hypothesizing that years in which adults were in higher condition would translate to years of higher quality offspring production which, in turn, have a higher probability of surviving and recruiting to age 3. Our analyses revealed marginal support for the positive effect of adult condition on recruitment. During the late 1960s and late 1990s, bloater condition was increasing, likely because of decreasing bloater population size and reductions in density-dependent effects. During these time periods only, the coefficients for adult condition in the top-ranked models were greater than zero. One concern for future recruitment, however, is that adult condition achieved considerably higher levels in the 1970s (before the resurgence in recruitment) than in the late 1990s and early 2000s (prior to when recruitment should resurge if bloater recruitment cycles). The recent decline of *Diporeia* spp. in Lake Michigan (Nalepa et al. 1998), one of the two primary prey items (along with *Mysis*) for adult bloaters (Crowder and Crawford 1984; TeWinkel and Fleischer 1999), likely explains the lower-than-expected adult condition in recent years. If bloaters resume a phase of high recruitment in spite of relatively low adult condition factors, then the hypothesis for adult condition as an internal factor regulating bloater recruitment will have even less empirical support.

Over the next 5–10 years, our annual GLSC bottom trawl surveys will reveal whether bloater recruitment in Lake Michigan returns to a high phase. If it does, then the proposed 30-year population cycle for bloaters (Madenjian et al. 2002) would be validated. If it does not, then we should consider the possibility that a "regime shift" in Lake Michigan has occurred (sensu Beamish et al. 1999) such that strong bloater recruitment is no longer supported in this ecosystem. Regardless of the findings of future surveys, however, our current study marked the first attempt to rigorously identify the important factors affecting bloater recruitment. Over a 38-year time series, a strong positive linkage between a balanced sex ratio and bloater reproductive success was revealed. Hence, bloaters are relatively unique among fish populations in that they appear to be regulated by a factor intrinsic, rather than extrinsic, to their population. However, additional research will be required to elucidate the mechanisms underlying this linkage.

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Bacterioplankton production, abundance, and nutrient limitation among lakes of the Mackenzie Delta (western Canadian arctic)

Bryan M. Spears and Lance F.W. Lesack

Abstract: The effects of nutrient availability and quality of dissolved organic carbon (DOC) on bacterioplankton production were assessed in six lakes with differing frequencies of river flooding. Bacterial productivity, dissolved nutrients, and DOC were tracked weekly throughout the open-water period of 2001. Inorganic nutrient (N and P) enrichment microcosm experiments were conducted to directly assess the effects of DOC quality (i.e., mixtures of colored and noncolored DOC) and inorganic nutrient limitation on bacterial productivity among the lakes. Averaged over the open-water season, both abundance and production of bacterioplankton increased with decreasing flood frequency (R^2 = 0.61 and R^2 = 0.78, respectively). Reduced bacterial production occurred in frequently flooded lakes, where colored DOC, light attenuation, and phosphate were high but ammonium was low. Bacterial production was greatest in infrequently flooded lakes, where noncolored DOC and ammonium were high but phosphate was low. Bacterial production was enhanced by amendments of inorganic nutrients in duplicate experiments (two-factor analyses of variance). Production was also enhanced in response to higher concentrations of either colored or noncolored DOC following release from inorganic nutrient limitation. Size fractionated (<1 μm versus >1 μm) N-debt and P-debt bioassays typically showed demand for P and release of N by bacteria in all study lakes.

Résumé : Nous avons évalué les effets de la disponibilité des nutriments et de la qualité du carbone organique dissous (DOC) sur la production du bactérioplancton dans six lacs affectés par des fréquences différentes d'inondations fluviales. Nous avons suivi la productivité bactérienne, les nutriments dissous et le DOC à chaque semaine pendant la période d'eau libre en 2001. Nous avons mené des expériences d'enrichissement avec des nutriments inorganiques (N et P) dans des microcosmes afin d'évaluer directement les effets de la qualité du DOC (c'est-à-dire des mélanges de DOC coloré et non coloré) et les limitations exercées par les nutriments inorganiques sur la productivité bactérienne dans les différents lacs. Les moyennes de l'abondance et de la production du bactérioplancton pendant la période d'eau libre augmentent toutes deux en fonction inverse de la fréquence des inondations (respectivement, R^2 = 0,61 et R^2 = 0,78). Dans les lacs inondés fréquemment dans lesquels le DOC coloré, l'atténuation de la lumière et les phosphates sont élevés et l'ammonium peu important, la production bactérienne est réduite. La production bactérienne est maximale dans les lacs qui sont rarement inondés dans lesquels le DOC non coloré et l'ammonium sont importants et le phosphore rare. Les amendements avec des nutriments inorganiques dans des expériences appariées (analyse de variance à deux facteurs) stimulent la production bactérienne. La production est aussi favorisée par des concentrations accrues de DOC coloré ou de DOC non coloré après la libération d'une limitation par les nutriments inorganiques. Des bioessais de dettes de N et de dettes de P fractionnées en fonction de la taille (<1 μm par rapport à >1 μm) indiquent une demande de P et une libération de N chez les bactéries dans tous les lacs.

[Traduit par la Rédaction]

Introduction

The Mackenzie Delta consists of 25 000 lakes, spans 13 500 km^2, and is the second largest arctic delta on the planet (Mackay 1963). The limnology of the lakes is heavily governed by a gradient in the frequency with which lakes receive floodwater from the river (i.e., flood frequency). This aquatic regime has created multiple biogeochemical gradients. Decreasing degree of riverine influence (i.e., decreasing flood frequency) generally corresponds with increasing macrophyte biomass, total dissolved organic carbon, and water transparency and decreasing amounts of riverine nutrients (P and N) (Marsh and Lesack 1996; Lesack et al. 1998; Squires and Lesack 2003*b*). Our understanding of how such

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multiple gradients interact needs to be improved to facilitate the construction of predictive global change models (Rouse et al. 1997). Lakes of the Mackenzie Delta are relatively high in dissolved organic carbon (DOC; i.e., bacterial substrate), and the DOC varies as a function of the flood-frequency gradient. At present, publications on the controls of heterotrophic bacterioplankton (hereafter simply referred to as bacteria) dynamics in arctic lakes have been limited mostly to Alaska (e.g., Hobbie et al. 1983; Crump et al. 2003) and sporadic work in the eastern Canadian arctic (e.g., Vincent et al. 2000).

Teichreb (1999) initiated the first investigation on bacterioplankton among lakes of the Delta. He found that bacterial production in one well-studied lake (South Lake) was stimulated by experimental additions of humic-DOC (i.e., colored-DOC) extracts derived from lake sediments. However, he subsequently found that bacterial abundances (production not measured) in a set of 40 lakes declined in correspondence with increasing levels of lake DOC (i.e., decreasing flood frequency). This raised the question of why abundance decreased when increasing levels of carbon substrate were available for the bacteria? One obvious hypothesis is that bacterial production was indeed higher among lakes with higher levels of DOC but that the enhanced production was consumed by planktonic grazers. This has been addressed in a related investigation (Riedel 2002) and will be reported in a forthcoming publication. A second possibility is that bacterial production is inhibited by increased exposure to ultraviolet (UV) radiation in lakes of low flood frequency because they are generally more transparent (Squires and Lesack 2003*a*). This is presently being addressed in an ongoing investigation. A third hypothesis, and the focus of this paper, is that bacterial production is inhibited in lakes of low flood frequency, despite higher levels of DOC, because the bacteria become nutrient limited.

Bacterial communities require a suite of inorganic (e.g., phosphate and ammonium) and organic (e.g., organic carbon compounds) nutrients. Inorganic nutrient limitation of bacterial growth has seen much recent attention (e.g., Elser et al. 1995; Carlsson and Caron 2001; Hutchins et al. 2001). Recent comparative studies have addressed three main sources of nutrient limitation in bacteria. The first is limitation of bacterial production through phytoplanktonic regulation of dissolved organic carbon (Bird and Kalff 1984; Cole et al. 1988; Jansson et al. 1996). The second is inorganic-P limitation of bacterial production (Sommer 1989; Elser et al. 1995; Gurung and Urabe 1999). This is substantiated by a strong positive correlation between bacterial production and total P concentration, which helps to explain the much lower correlations between bacterial and phytoplankton biomass in systems where the total dissolved organic carbon pool (T-DOC) is high and therefore not limiting (Nuernberg and Shaw 1998). Recent studies have also reported direct P limitation of bacterial growth in lakes (Le et al. 1994; Coveney and Wetzel 1995). The third source is inorganic-N limitation of bacterial production. Although N limitation of bacterial growth has been observed in marine environments, it has seldom been observed in freshwater studies (Kirchman and Wheeler 1998).

Our understanding of the potential effects of DOC quality is less clear than our understanding of the effect of inorganic nutrient availability. Studies concerned with substrate lability have resulted in the categorization of two distinct pools of DOC (Lampert and Sommer 1996). These separate pools consist of a labile fraction (autochthonous DOC mainly derived from aquatic vegetation), with a possible turnover on the order of hours to days, and a refractory fraction (allochthonous DOC mainly derived from terrestrial vegetation from surrounding watershed), with a possible turnover on the order of weeks to months (Moran and Hodson 1990; Williamson et al. 1999). Autochthonous DOC (low in color) is mainly derived from within-lake processes, the main contributing process thought to be exudation by aquatic plants, in particular phytoplankton and macrophytes (Findlay et al. 2001). The wide variability of DOC composition is due to a variety of lake characteristics (e.g., topography, depth, geographic location, nutrient load) and results not only in a variation of T-DOC concentration, but also variations in the colored dissolved organic carbon (C-DOC) and noncolored dissolved organic carbon (NC-DOC) components (Williamson et al. 1999). Although C-DOC per se might be considered refractory, it readily absorbs UV irradiance and photochemically breaks down into labile compounds that can be exploited by bacteria (Moran and Hodson 1990; Bertilsson and Tranvik 2000). In an environment with 24-h daylight at the summer solstice, this could be an important source of carbon substrate for bacteria in lakes with high flood frequency (i.e., stronger riverine influence, high C-DOC, and high nutrients).

During the summer of 2001, the hypothesis that nutrient limitation inhibits bacterial production and potentially accounts for the pattern (Teichreb 1999) of high to low bacterial abundances among lakes ranging, respectively, from low to high T-DOC in the Mackenzie Delta was assessed. Patterns of bacterial productivity, dissolved nutrients, and DOC were tracked weekly in six lakes with differing frequencies of river flooding and differing mixtures of C- and NC-DOC. To directly assess potential nutrient limitation and differences in DOC quality (i.e., mixtures of C- and NC-DOC), bacterial productivity among lakes was experimentally compared via lab-incubated microcosms after amending with nutrients (N + P). Herein, we report the first results on patterns of bacterial production among delta lakes of the circumpolar arctic and the potential role of nutrient limitation and DOC quality in controlling the pattern.

Methods

Study area

The Mackenzie Delta is located where the Mackenzie River discharges into the Beaufort Sea and is a complex system containing about 25 000 lakes. The Mackenzie River flows north spanning a temperature gradient of relative warmth to a colder environment (Mackay 1963). This northerly flow causes extensive ice jamming during spring breakup, which results in the main annual flooding event of Mackenzie Delta lakes with secondary peaks occurring as a result of sporadic summer rains (Marsh and Hey 1989).

The hydrological character of Mackenzie Delta lakes may be split into three distinct categories by considering sill elevation (highest point on the thalweg of the connection between river and lake). In a survey of 132 lakes in a middle

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section of the Mackenzie Delta, 12% were frequently flooded (sill elevation < 1.5 m above sea level (asl)), 55% were intermediately flooded (sill elevation between 1.5 and 3.5 m asl), and 33% were infrequently flooded (>3.5 m asl) (Marsh and Hey 1989). Because annual precipitation occurs in near-desert amounts (266 mm at Inuvik), the dominant component of the water balance of Mackenzie Delta lakes is flooding by the river (Marsh and Lesack 1996). Transport of water out of the lake is mainly evaporation, because of the presence of permafrost beneath the drainage basin and the relatively low permeability of the sediments (Marsh and Hey 1989). Thus, flood frequency plays an essential role both in the periodic replenishment of essential nutrients and in governing the dynamics of a lake's water balance.

Six lakes were chosen on merit of sill elevation (Fig. 1), so that two lakes from each flood-frequency class (frequently, intermediately, and infrequently flooded) were studied over an 8-week period (20 June to 8 August 2001). The gradient of sill elevation, lake area, flood-frequency categorisation, maximum depth recorded at the sample location, and mean depth of the six lakes are summarized (Table 1). The selected lakes ranged in mean depth from about 1 m to about 2.3 m and are representative of lake depths in the central Mackenzie Delta (Lesack et al. 1998; Squires and Lesack 2002). Because the lakes are shallow, they are well mixed and do not thermally stratify during the open-water season.

Field and laboratory techniques

Integrated water samples (1 m depth) were collected using a tube sampler (67 mm internal diameter and 1 m length) and stored in a cooler in acid-washed Nalgene bottles during transport to the laboratory. Samples for bacterial enumeration were collected and preserved with formalin (2% final concentration).

In situ vertical profiles (0.5 m intervals) of temperature and conductivity (YSI 3000 T-L-C model field conductivity probe; YSI Inc., Yellow Springs, Ohio) and photosynthetically active radiation (Li-Cor photometer equipped with an underwater quantum sensor; Li-Cor Inc., Lincoln, Nebraska) were obtained at the time of sampling and used to construct average conditions throughout the water column. Weekly vertical light extinction coefficients (Kd) were calculated according to the protocol of Fee et al. (1988). Temperature-corrected (ATC probe; Orion, Thermo Electron Corporation, San Jose, California) pH readings were taken using a 290A pH meter (Orion, Thermo Electron Corporation) within 24 h of sampling. Total suspended sediments were quantified according to Stainton et al. (1977). Water for PO_4^{3-} and NH_4^+ analysis was filtered (within 6 h of collection) through a Whatman GF/C filter and stored in acid-cleaned plastic bottles at 4 °C until analysis. The filtrates were then processed (within 12 h) using colorimetric techniques described by Stainton et al. (1977).

Measurement of T-DOC was done on GF/C-filtered (within 6 h of collection) water, which was stored at –4 °C preceding T-DOC analysis. Samples were shipped to the Freshwater Institute (Department of Fisheries and Oceans, Winnipeg, Manitoba) where T-DOC concentration was analysed using an acid persulfate oxidation technique, and the released CO_2 was subsequently measured by an infrared detector. Prior testing of GF/C filtration versus filters with smaller pore sizes has well established that the carbon content of bacteria capable of passing through GF/C filters is an insignificant component of the overall levels of DOC in this study system.

Estimation of C-DOC concentrations was done spectrophotometrically by measuring the optical absorbance of 0.22 µm (Millipore polycarbonate membrane) filtered water samples in a 10 cm quartz cuvette. Absorbances at 330 nm were corrected for background scatter by subtracting the corresponding absorbance at 740 nm. Scatter-corrected absorbances at 330 nm were subsequently converted to an attenuation coefficient Ka330 by standardizing the absorbance per metre of water and converting it to natural logarithms. We primarily report the index Ka330 as a measure of C-DOC in this paper for consistency with other publications on the Mackenzie Delta. For interpreting the two nutrient-enrichment experiments and understanding the DOC gradient among the 6 lakes, the Ka330 index was converted to an analogous value at 310 nm using the precise empirical relation between absorbance at 330 nm and absorbance at 310 nm in lakes of the delta (based on 1 nm band width scans over the wavelength range with a Thermospectronic Genesys 5 spectrophotometer; Thermo Electron Corporation), and then an approximate estimate of C-DOC concentration was obtained from the relation between Ka310 and DOC concentration published by Scully and Lean (1994; assumes C-DOC = DOC in that study). NC-DOC was estimated as the difference between T-DOC and C-DOC. Where we have reported inferred C-DOC and NC-DOC concentrations in micromoles per litre ($\mu mol \cdot L^{-1}$), we acknowledge uncertainty associated with these empirically derived estimates.

Fractionated phytoplankton biomass was estimated using the guidelines underpinned by Sieburth et al. (1978). Phytoplankton of cell diameter < 20 µm are considered edible by zooplankton, whereas phytoplankton of cell diameter > 20 µm are considered inedible. Size fractionation was carried out by prescreening total lake water through a 20 µm Nytex mesh (Sefar Canada Inc., Ville St-Laurent, Quebec) before pigment analysis of total and the <20 µm filtrate according to Stainton et al. (1977).

Samples for bacterioplankton enumeration and production were prescreened through a GF/C filter to remove any sediment-attached organisms. Therefore, the reported abundances can be used as an index of abundance for bacterioplankton but do not reflect the true abundance of the full bacterial community in the water column. Bacterial enumeration was carried out according to the methods described by Porter and Feig (1980). Enumeration was carried out using a Carl Zeiss Axioplan epifluorescent microscope (Carl Zeiss, New York) fitted with a HBO 50 mercury lamp and BG38 and KG1 red-free filters. A G365 exciter filter, FT395 chromatic beam splitter, and LP420 barrier filter were used to allow the DAPI-stained cellular DNA to be viewed. Slides were counted in the dark with 10 fields or at least 100 individual cells being counted at 1000× magnification using a 100/1.3 Plan-Neofluor oil objective lens and a 10× eyepiece with graticule. Total bacterial numbers per millilitre were calculated as described by Sherr et al. (1993).

Bacterial production was quantified using the tritiated thymidine ([^{3}H]TdR) incorporation method as described by Robarts (1998). Bacterioplankton productivity was calculated

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Fig. 1. Map of study area in the Mackenzie Delta, western Canadian arctic (inset).

from the rates of [^{3}H]TdR incorporation using the equation described by Wetzel and Likens (2000). Estimates of bacterial production per cell were obtained by dividing the bacterial production results with the corresponding bacterial abundance data.

Inorganic nutrient enrichment experiments

The patterns of NC-DOC and C-DOC among lakes of differing flooding frequencies were used to construct two microcosm experiments designed to investigate the relative nutritional value of both classes of DOC. Although T-DOC values in Mackenzie Delta lakes are known to be high (Squires and Lesack 2003*a*), concentrations of a preferential carbon substrate, be it colored or noncolored, may be low. Natural variations in DOC were tracked and used to design nutrient-enrichment experiments in which the ratio of C-DOC to NC-DOC was used to compare bacterial production over a gradient of (*i*) increasing C-DOC with similar NC-DOC (experiment 1, 17 July 2001) and (*ii*) increasing NC-DOC with constant C-DOC (experiment 2, 31 July 2001). Inorganic nutrient enrichment was carried out to remove potential resource limitation by P or N. We expected the highest bacterial production under a DOC regime in which NC-DOC was highest and C-DOC was lowest. This would be consistent with the hypothesis that NC-DOC was the favourable carbon source.

Water was collected from three carefully selected lakes, on the day of each enrichment experiment, using a 1 m inte-

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Table 1. Information pertaining to the physical characteristics of each of the six lakes sampled.

	Lake					
	South	80	87	280	56	520
Sill[a]	2.36	2.63	3.39	3.84	4.62	4.91
Flood freq.[c]	FF	FF	IF	IF	INF	INF
Area[d]	0.378	0.193	0.039	0.024	0.031	0.002
Mean depth	1.29	1.52	1.31	1.64	1.08	2.23
Max. depth[b]	2.64	2.54	1.82	2.38	0.76	3.21

Note: Sill, sill elevation (metres above sea level (m asl); Flood freq., flood-frequency category (FF, frequently flooded lakes of sill elevation < 1.5 m asl; IF, intermediately flooded lakes of sill elevation between 1.5 and 3.5 m asl; INF, infrequently flooded lakes of sill elevation > 3.5 m asl); Area, lake area (m^2); mean depth (m); Max. depth, the maximum depth (m) recorded at the sample location.

[a]Marsh and Hey 1989.

[b]Squires et al. 2002.

grated tube sampler. For each lake, 20 L of water was prescreened through a 200 µm Nytex mesh to remove any microzooplankton and stored for up to 2 h in a 20 L carboy in a cooler. Triplicate 2 L transparent Nalgene bottles were filled with filtered lake water and placed in an incubator under controlled light and temperature conditions to acclimatize for 30 min. The temperature of the incubator was set to the average ambient temperature of the three lakes. The average ambient temperatures were 19.7 °C and 15.2 °C on 17 and 31 July, respectively.

After acclimatization, triplicate initial samples for bacterial productivity and bacterial biomass were removed from each of the nine 2 L Nalgene bottles. Immediately after the removal of the initial samples, each bottle was spiked with excess amounts of inorganic nitrogen (10 µmol·L^{-1} NH_4Cl) and phosphorus (10 µmol·L^{-1} KH_2PO_4). These concentrations were chosen to be sufficiently high to ensure relief of possible N or P limitation in the bacterial community and ensure that the response of the bacteria reflected their ability to use the DOC substrate available to them. The enrichment concentrations were well below levels that would affect the ionic strength of waters in the Mackenzie Delta (see Lesack et al. 1998). The concentrations were also intended to match the procedure for N- and P-debt bioassays carried out on the plankton community during this study (procedure of Healey and Hendzel 1980), as described in the following section. The incubation was then allowed to proceed for 2 h to minimize the potential effects of heterotrophic nanoflagellate grazing before removing final triplicate samples from each bottle for bacterial productivity and biomass quantification.

Modified N- and P-debt bioassays

These experiments were designed to investigate the extent of inorganic nutrient limitation of bacterial productivity across the flood-frequency gradient and were carried out on the same dates as the nutrient-enrichment experiments described above. The assays provide an indication of the nutritional status of the plankton and are based on the methods of Healey and Hendzel (1980) and Gerhart and Likens (1975). Modifications were made to allow quantification of bacterioplankton nutrient limitation by first prescreening whole-lake water through a Whatman GF/C filter to remove the effects of larger plankton. The filtrate was then saturated with N (10 µmol·L^{-1} NH_4Cl) and P (10 µmol·L^{-1} KH_2PO_4), and nutrient uptake was allowed to proceed in the dark at room temperature for 24 h. The incubations were terminated by filtration (0.1 µm nitrose–cellulose filter) immediately after addition of nutrients and at the end of the 24-h incubation, with total nutrient uptake being indicative of N or P deficiency. Uptake and release values were corrected to bacterial abundance.

Statistical analysis

Average values for each of the lakes were calculated over the 8-week sampling period. The relations between measured variables and lake sill elevation were assessed using linear regression analyses.

Variations in the responses of each lake in the inorganic nutrient enrichment experiments were analysed using two-way analysis of variance (ANOVA, $\alpha = 0.05$). In preparation for a significant ANOVA result, planned comparisons of the enrichment experiment included (*i*) between nutrient-enriched and nutrient-unenriched water and (*ii*) across a gradient of high to low NC-DOC or C-DOC. Statistical design was conducted in accordance to Sokal and Rohlf (1995).

Results

Physical and chemical characteristics of the study lakes

The study lakes collectively represent a dynamic multigradient system, largely driven by differing frequencies of flooding with river water as a function of the sill elevations of the lakes. The particular gradients in place at the time of our investigation need to be specified to interpret the responses of the bacterioplankton community. The extent of these gradients is shown in the form of linear regression analysis between the measured variables and lake sill elevation (Table 2). Among the six lakes, water transparency, as indicated by light attenuation (Kd), decreased ($R^2 = 0.75$) with increasing sill elevation (Fig. 2*a*). This relation is consistent with previous work (Squires and Lesack 2003*a*; Teichreb 1999) and is coupled with decreases in total suspended sediments (TSS) and C-DOC ($R^2 = 0.75$ and $R^2 = 0.81$, respectively, during this study) as sill elevations increase and, ultimately, river-water inputs decrease.

The gradients of PO_4^{3-} ($R^2 = 0.75$) and NH_4^+ ($R^2 = 0.47$) generally ran counter to one another as lake flooding frequency decreased (Figs. 2*b* and 2*c*, respectively). Averaged over the open-water season, PO_4^{3-} decreased and NH_4^+ increased with decreasing flood frequency. This pattern is con-

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Table 2. Summary of statistical relationships between the mean open-water values of measured variables and lake sill elevation; between bacterial production per cell and C-DOC, NC-DOC, TSS, and lake temperature; and between C-DOC and TSS, lake temperature, and NC-DOC during 2001.

Relationship	*P* value	R^2	Slope	Intercept
Relationship with lake sill elevation				
Kd vs. Sill	0.026	0.75	–0.314	2.57
TSS vs. Sill	0.026	0.75	–0.0023	0.111
PO_4^{3-} vs. Sill	0.025	0.75	–0.014	0.099
T-DOC vs. Sill	0.035	0.71	166	206
C-DOC vs. Sill	0.014	0.81	–1.85	20.7
NC-DOC vs. Sill	0.022	0.77	204	–500
BacAbun vs. Sill	0.066	0.61	1.37	1.27
Prod/cell vs. Sill	0.019	0.78	13.78	–14.83
Relationship with bacterial production per cell				
Prod/cell vs. C-DOC	0.019	0.78	–6.7	129.3
Prod/cell vs. TSS	0.034	0.71	–4848.0	532.7
Prod/cell vs. T	0.060	0.63	27.02	–403.3
Prod/cell vs. NC-DOC	NS	0.44	Positive Slope	
Relationship of C-DOC with TSS, T, and NC-DOC				
C-DOC vs. TSS	0.0025	0.92	Positive slope	
C-DOC vs. T	0.014	0.81	Negative slope	
C-DOC vs. NC-DOC	0.019	0.78	Negative slope	

Note: Sill, lake sill elevation (metres above sea level); Kd, light attenuation (m^{-1}); TSS, total suspended sediments ($g \cdot L^{-1}$); PO_4^{3-}, soluble reactive phosphate concentration ($\mu g \cdot L^{-1}$); T, lake temperature (°C); T-DOC, total dissolved organic carbon ($\mu mol \cdot L^{-1}$); C-DOC, colored dissolved organic carbon (Ka330); NC-DOC, noncolored dissolved organic carbon ($\mu mol \cdot L^{-1}$); BacAbun, bacterial abundance (1×10^9 cells·mL^{-1}); Prod/cell, bacterial production per cell (1×10^{-15} mol TdR·cell^{-1}·h^{-1}); NS, not significant.

sistent with prior work and occurs because the two nutrients have differing sources. The largest source of PO_4^{3-} to lakes of the Delta is typically from riverine inputs, with background noise in the signal being maintained by biotic cycling of organic forms of P within the lakes. On the other hand, NH_4^+ is typically low in river water and instead is supplied via breakdown of organic matter and excretion by organisms within the lakes. Abiotic and biotic ammonification is known to occur, and size-fractionated N-debt experiments conducted in this study indicated that bacteria, at typical lake-water abundances, were capable of excreting up to 2 µmol NH_4^+ per litre of lake water in 24 h. Thus, the pattern of increasing NH_4^+ with decreasing flood frequency may reflect higher rates of ammonification by bacteria.

The average gradients of T-DOC and C-DOC also ran counter to one another as lake flooding frequency decreased. Averaged over the open-water season, T-DOC concentrations increased with sill elevation ($R^2 = 0.71$; Fig. 2*d*), with Lake 80 showing the lowest (630 µmol·L^{-1}) and Lake 520 the highest (1190 µmol·L^{-1}) T-DOC concentration. C-DOC, however, decreased as flood frequency decreased ($R^2 = 0.81$; Fig. 2*e*). Lake 80 had the highest (Ka330 = 16.4) and Lake 520 the lowest (Ka330 = 11.4) C-DOC. Additionally, NC-DOC increased with sill elevation ($R^2 = 0.77$; Fig. 2*f*). As was the case with inorganic nutrients, this pattern is produced because the two forms of DOC have differing sources in this delta system. C-DOC comes mainly from river inputs (thus associated with increasing flooding frequency), whereas NC-DOC seems to be derived mostly from macrophytes (associated with decreasing flooding frequency; Squires et al. 2002) and other autotrophs directly within the lakes of this system.

Bacterioplankton abundance and production

In contrast to the pattern obtained by Teichreb (1999) during a prior investigation, bacterial abundance, averaged over the open-water season for each lake (Fig. 3*a*), increased with decreasing flood frequency ($R^2 = 0.61$). The lowest bacterial abundance was observed in South Lake (3.93×10^9 cells·mL^{-1}) and the highest was observed in Lake 87 (8.16×10^9 cells·mL^{-1}). The abundances are low relative to values typically reported in other freshwater systems and relative to other work we have done in this system (Teichreb 1999; Febria 2005). A primary reason for the lower abundances is that we made a conscious decision to exclude particle-bound bacteria in the present study by filtering the community through a GF/C filter before taking samples for cell counts. These results represent an appropriate index of abundance for the bacterioplankton in this system (see Discussion) but do not reflect the true abundance of the full bacterial community. However, regression analysis, carried out on the mean open-water values for bacterial abundance, showed no significant relation with per cell rates of bacterial production or with any of the measured variables.

When Teichreb (1999) previously documented a pattern of decreasing bacterial abundance with increasing lake sill elevation, it was not known whether the pattern was a consequence of declining bacterial production or some other factor. In our present investigation, bacterial production per cell, averaged over the open-water season for each lake, in-

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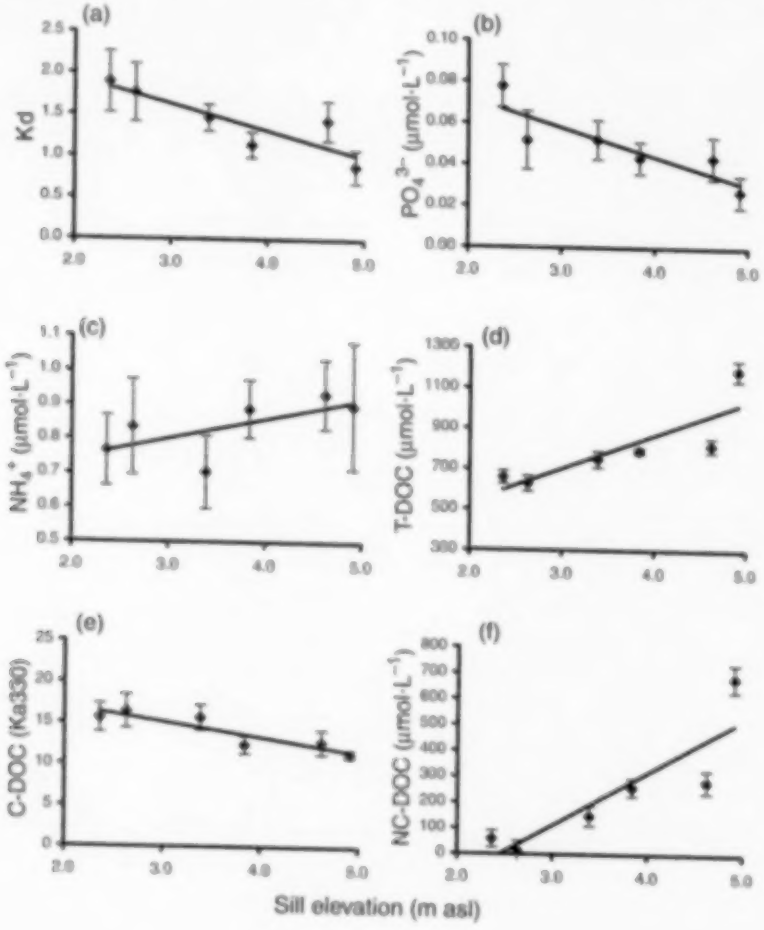
Fig. 2. (*a*) Relationship between average Kd and sill elevation (metres above sea level (m asl); Marsh and Hey 1989) for the six lakes (R^2 = 0.75). (*b*) Relationship between average PO_4^{3-} concentration and sill elevation for the six lakes (R^2 = 0.75). (*c*) Relationship between average NH_4^+ concentration with sill elevation for the six lakes (R^2 = 0.47). (*d*) Relationship between total dissolved organic carbon (T-DOC) and sill elevation for the six lakes (R^2 = 0.71). (*e*) Relationship between colored dissolved organic carbon (C-DOC) and sill elevation for the six lakes (R^2 = 0.81). (*f*) Relationship between non-colored dissolved organic carbon (NC-DOC) and sill elevation for the six lakes (R^2 = 0.77).



creased with increasing sill elevation (R^2 = 0.78; Fig. 3*b*), with Lake 56 having the highest production per cell (58.3 × 10^{-17} mol TdR·cell^{-1}·h^{-1}) and Lake 87 having the lowest (16.7 × 10^{-17} mol TdR·cell^{-1}·h^{-1}).

Although sill elevation is a composite variable related to multiple covarying factors (Table 2), per cell bacterial production responded inversely, but equally strongly, to C-DOC (R^2 = 0.78) and less strongly to TSS (R^2 = 0.71) and lake temperature (R^2 = 0.63) (Fig. 4). None of the other variables related to sill elevation was significantly related to per cell production. C-DOC, TSS, and lake temperature all appear to be strongly intercorrelated (Table 2) and, consequently, will not yield a viable multiple regression model. C-DOC is, however, inversely and strongly related to NC-DOC and suggests that NC-DOC ought to be positively related to per cell bacterial production. This also suggests that NC-DOC may be the favoured carbon substrate in this system; however, the relation between per cell production and NC-DOC is not significant.

Nutrient-enrichment and carbon quality experiments

The response in bacterial production per cell following inorganic nutrient enrichment during experiment 1 (17 July 2001) and the associated N- and P-debt bioassays of potential bacterial nutrient demand are shown (Fig. 5). A summary of the levels of DOC composition among the experimental lake waters is also shown (Table 3). At that time, C-DOC levels were not greatly different among the lakes, but Lake 280 (520 µmol·L^{-1}) was modestly lower than either Lake 87 or South Lake (560 and 570 µmol·L^{-1}, respectively). On the other hand, NC-DOC was similar in Lakes 87 and 280 (290 and 270 µmol·L^{-1}, respectively), whereas it was substantially

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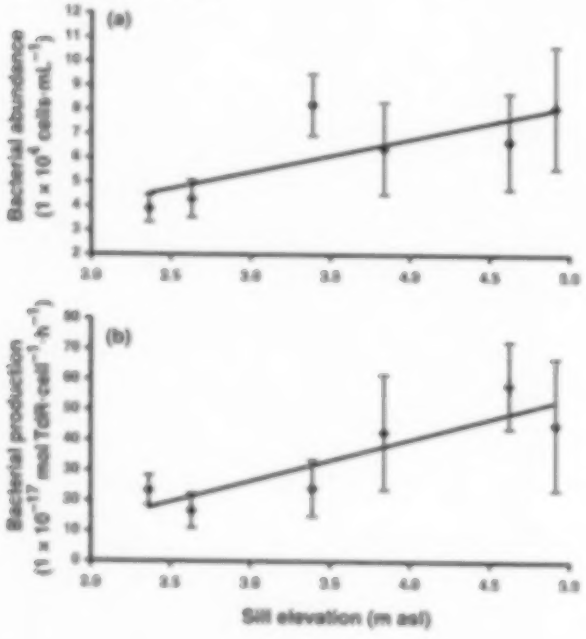
Fig. 3. (*a*) Relationship between bacterial abundance (1×10^4 cells·mL^{-1}) and sill elevation (metres above sea level (m asl); Marsh and Hey 1989) ($R^2 = 0.61$). (*b*) Relationship between bacterial production per cell (1×10^{-17} mol TdR·cell^{-1}·h^{-1}) and lake sill elevation ($R^2 = 0.78$).

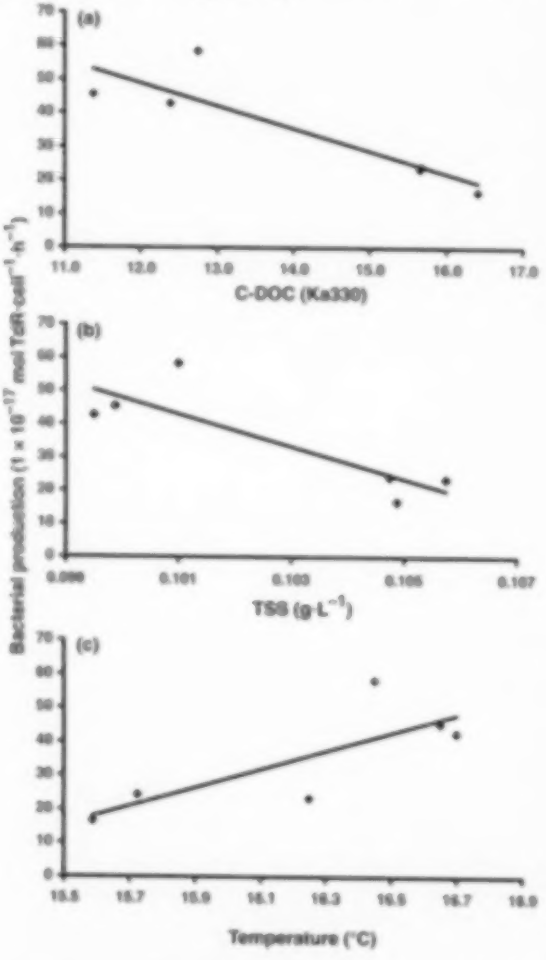


lower in South Lake (90 μmol·L^{-1}) at that time. Under this C-DOC – NC-DOC regime, if inorganic nutrient limitation is removed, Lakes 87 and 280 would be expected to show a greater increase in bacterial production than South Lake if NC-DOC was of better nutritional quality than C-DOC. Alternatively, if C-DOC was of better nutritional quality, South Lake or Lake 87 should respond more strongly than Lake 280 to the removal of inorganic nutrient limitation.

At the time of experiment 1, nutrient-debt bioassays showed that bacteria in South Lake and Lake 280 may have been P-limited at that time and that no lakes were N-limited. Bacterial P uptake ranged from 3.2% of the total community uptake by heterotrophic and autotrophic plankton (i.e., unfiltered lake water) in South Lake to ~100% in Lake 280. P release was observed in Lake 87. All lakes released N. Before nutrient enrichment, bacterial abundance was highest in Lake 87 (5.6×10^4 cells·mL^{-1}) and lower in South Lake and Lake 280 (2.7×10^4 and 2.3×10^4 cells·mL^{-1}, respectively). Lake 87 was lowest in bacterial production per cell (2.33×10^{-17} mol TdR·cell^{-1}·h^{-1}), South Lake had intermediate production per cell (6.83×10^{-17} mol TdR·cell^{-1}·h^{-1}), and Lake 280 was highest in production per cell (8.20×10^{-17} mol TdR·cell^{-1}·h^{-1}).

Following nutrient enrichment, production per cell increased in all lakes, with Lake 87 showing the largest increase (109%), followed by South Lake (82%), and then Lake 280 (29%). This particular response (see above) is consistent with C-DOC being preferred over NC-DOC. The large increase in production in Lake 87 was not expected based on N- and P-debt results that showed Lake 87 releasing significant NH_4^+ and possibly a small amount of PO_4^{3-} (amount may not have been significant), whereas Lake 280 had the weakest response despite a P-dept result that indicated significant uptake of P. The response in production per cell in South Lake and Lake 280 can be explained by N- and P-debt results, where the largest response is observed with the highest amounts of nutrient uptake. These results, however, also indicate that Lake 87 should not be limited by inorganic nutrients. A fixed-effect, two-way ANOVA (total df = 17) confirmed that C-DOC levels and inorganic nutrient enrichment each had significant effects on bacterial production ($p = 0.0002$ and $p = 0.0017$, respectively), but that the potential interactive effect of C-DOC plus inorganic nutrient enrichment was not significant ($p = 0.354$).

Fig. 4. (*a*) Relationship between bacterial production per cell (1×10^{-17} mol TdR·cell^{-1}·h^{-1}) and C-DOC (Ka330) ($R^2 = 0.78$, $p = 0.019$). (*b*) Relationship between bacterial production per cell (1×10^{-17} mol TdR·cell^{-1}·h^{-1}) and total suspended sediments (g·L^{-1}) ($R^2 = 0.71$, $p = 0.034$). (*c*) Relationship between bacterial production per cell (1×10^{-17} mol TdR·cell^{-1}·h^{-1}) and water temperature (°C) ($R^2 = 0.63$, $p = 0.06$).



In experiment 2 (31 July 2001), the response in bacterial production per cell following inorganic nutrient enrichment

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Fig. 5. Results from the inorganic nutrient enrichment experiment carried out on 17 July 2001 for South Lake, Lake 87, and Lake 280 showing (*a*) levels of bacterial production per cell (1×10^{-17} mol TdR cell^{-1} h^{-1}) before (solid bars) and after (shaded bars) inorganic nutrient enrichment, (*b*) percent change in bacterial production per cell following inorganic nutrient enrichment, (*c*) modified P-debt results indicating uptake or release of phosphate (μmol 10^4 cells·day^{-1}) by bacteria, and (*d*) modified N-debt results indicating uptake (positive values) or release (negative values) of ammonium (μmol per 10^4 cells per day) by bacteria.

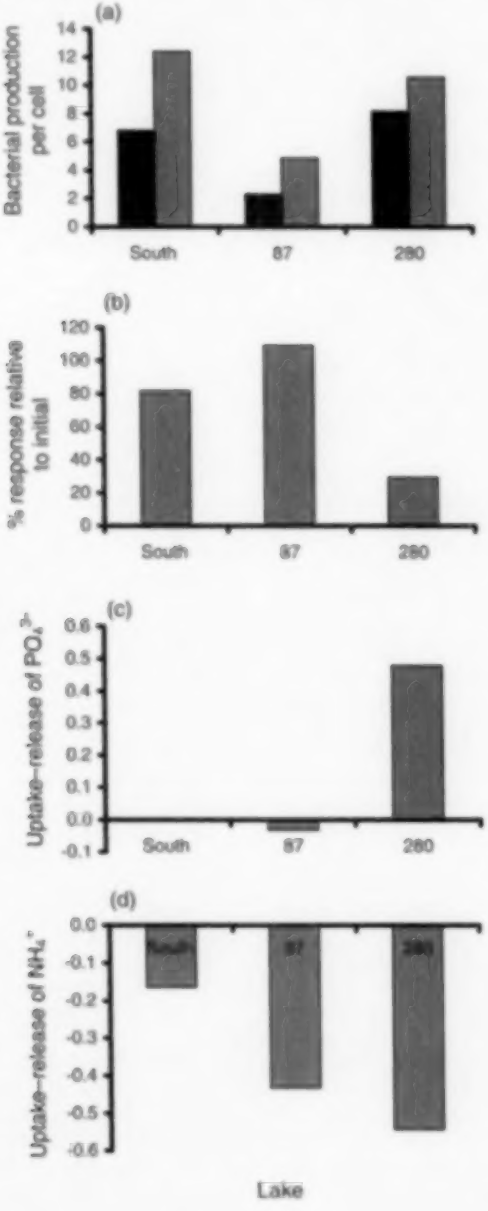

Table 3. Initial levels (μmol·L^{-1}) of total dissolved organic carbon (T-DOC), colored dissolved organic carbon (C-DOC), and noncolored dissolved organic carbon (NC-DOC) in the lakes included in the inorganic nutrient enrichment experiments conducted on 17 and 31 July 2001.

Lake	T-DOC (μmol·L^{-1})	Ka330 (m^{-1})	C-DOC (~μmol·L^{-1})	NC-DOC (~μmol·L^{-1})
Experiment 1, 17 July 2001				
South Lake	660	14.1	570	90
Lake 87	850	14.0	560	290
Lake 280	790	11.7	520	270
Experiment 2, 31 July 2001				
South Lake	500	11.0	500	~0
Lake 280	750	11.0	500	250
Lake 520	1130	11.1	500	630

Note: Concentrations of T-DOC were measured directly, C-DOC was estimated via measurements of optical absorbance (A330 nm) and an empirical relation between Ka330 and C-DOC concentration, and NC-DOC = T-DOC – C-DOC. Concentrations of C-DOC and NC-DOC are thus only approximate.

and the associated N- and P-debt bioassays of potential bacterial nutrient demand are shown (Fig. 6). This case represented a well-defined gradient of increasing NC-DOC (South Lake = ~0 μmol·L^{-1}, Lake 280 = 250 μmol·L^{-1}, and Lake 520 = 630 μmol·L^{-1}) at a time when C-DOC was around 500 μmol·L^{-1} in each of the lakes. Under this C-DOC – NC-DOC regime, if inorganic nutrient limitation is removed, Lake 520 ought to show the strongest response in per cell bacterial production, with respectively weaker responses by Lake 280 and South Lake, if NC-DOC is readily utilized by the bacterial community. At the time of experiment 2, nutrient-debt bioassays indicated that bacteria in Lakes 280 and 520 ought to have the highest possibility of being P-limited, while none of the lakes showed signs of N limitation. Bacterial P uptake ranged from 6.18% of total community uptake in Lake 520 to ~100% in Lake 280. P release was observed in South Lake. Bacteria in all lakes released NH_4^+. Before nutrient enrichment, bacterial abundance increased with sill elevation, ranging from South Lake (6.3×10^4 cells·mL^{-1}) to Lake 520 (10.3×10^4 cells·mL^{-1}). Bacterial production per cell was highest in Lake 280 (22.9×10^{-17} mol TdR·cell^{-1}·h^{-1}) and lower in South Lake (10.5×10^{-17} mol TdR·cell^{-1}·h^{-1}) and Lake 520 (5.75×10^{-17} mol TdR·cell^{-1}·h^{-1}).

After nutrient enrichment, production per cell increased in all the lakes, with a progressively stronger response occurring as the inferred level of NC-DOC increased (i.e., South Lake = +25%, Lake 280 = +138%, Lake 520 = +156%). This is consistent with NC-DOC representing a fully viable substrate for the bacterial community in these lakes. It appears, however, that the response may plateau as NC-DOC increases to high values. This may indicate a point at which bacterial production becomes saturated by carbon substrate. A fixed-effect, two-way ANOVA (total df = 17) confirmed that NC-DOC levels and inorganic nutrient enrichment each had significant effects on bacterial production ($p < 0.0001$ and $p = 0.0002$, respectively) and that the interactive effect of NC-DOC plus inorganic nutrient enrichment was also significant ($p = 0.0017$).

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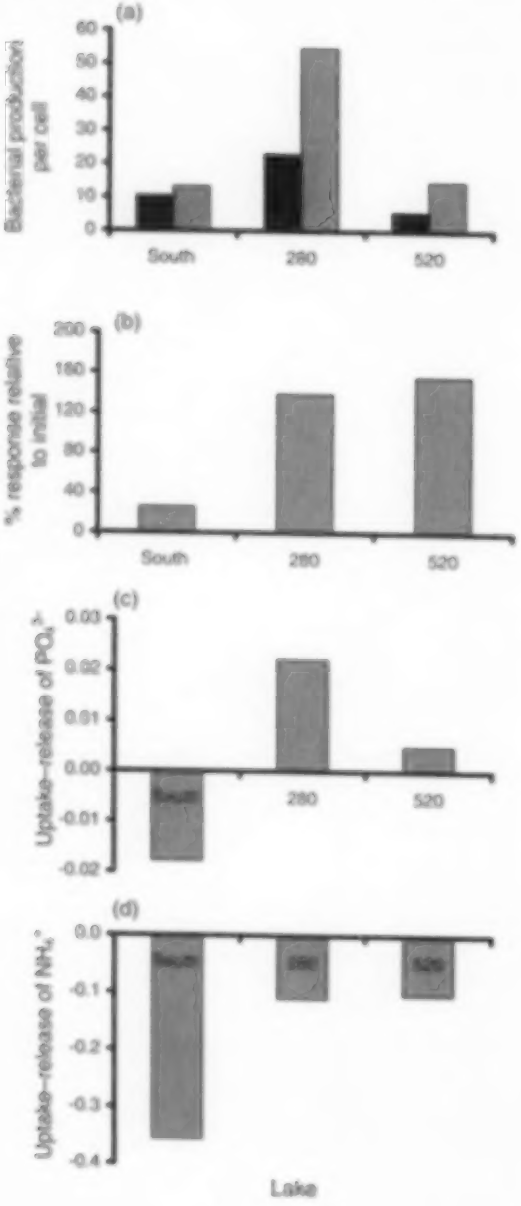
Fig. 6. Results from the inorganic nutrient enrichment experiment carried out on 31 July 2001 for South Lake, Lake 280, and Lake 520 showing (*a*) levels of bacterial production per cell (1×10^{-17} mol TdR·cell^{-1}·h^{-1}) before (solid bars) and after (shaded bars) inorganic nutrient enrichment, (*b*) percent change in bacterial production per cell following inorganic nutrient enrichment, (*c*) modified P-debt results indicating uptake or release of phosphate (μmol 10^4 cells·day^{-1}) by bacteria, and (*d*) modified N-debt results indicating uptake (positive values) or release (negative values) of ammonium (μmol per 10^4 cells per day) by bacteria.



Discussion

General patterns of bacterial abundance and production

Before initiating studies of bacterial dynamics in the Mackenzie Delta, we postulated that bacterioplankton production ought to track the generally observed DOC gradient (Lesack et al. 1998) from low levels in frequently flooded lakes to high levels in infrequently flooded lakes. Teichreb (1999) subsequently initiated bacterial work in the Delta and unexpectedly reported declining bacterial abundances with decreasing flooding frequency. In the present study, both bacterial abundance and production per cell were found to increase with decreasing flood frequency and are thus inconsistent with Teichreb's (1999) findings but appear to be consistent with our original hypothesis. Additionally, during the present study, C-DOC was shown to decrease with decreasing flood frequency, whereas Teichreb (1999) reported an increase in C-DOC with decreasing flood frequency. So why are the respective results inconsistent? The pattern of bacterial abundance and C-DOC reported in Teichreb's (1999) study was based on a late summer (beginning of September) survey of 40 lakes (a synoptic snapshot) in the Inuvik area of the Mackenzie Delta. Basic data on those lakes have been tracked on and off since the late 1980s (e.g., Lesack et al. 1998; Squires and Lesack 2003*a*). On the other hand, the main purpose of this study was to assess the average conditions of bacterial production over the full open-water period by focussing on a smaller number of lakes. The patterns of bacterial abundance and C-DOC reported by Teichreb (1999) could be either a later summer phenomenon and (or) a result of differences in the average characteristics of the 40 lakes in his study relative to the six lakes in the present study. Alternatively, Teichreb's pattern (lower bacterial abundances in lakes with higher C-DOC) does suggest that C-DOC may be a less efficient substrate for bacteria, and this result could be considered consistent with that of the present study, even though the pattern with sill elevation is not.

Averaged over the open-water season, bacterial abundance increased with decreasing flood frequency. In a related 15-lake "snapshot" survey (Riedel 2002), heterotrophic nanoflagellate abundance was observed to increase with decreasing bacterial abundance, suggesting evidence of a trophic cascade. Therefore, grazing pressure, via heterotrophic nanoflagellates, can at least sporadically range from high in frequently flooded lakes to low in infrequently flooded lakes. Teichreb's (1999) trend of decreasing bacterial abundance with decreasing flood frequency may therefore be a result of a gradient of grazing pressures and not nutrient limitation. Additionally, both surveys reported correlation between C-DOC and bacterial abundance, suggesting that C-DOC is an unfavourable carbon substrate.

The pattern of increasing per cell bacterial production with decreasing flood frequency matches what we originally postulated to find in this lake system, but the underlying factors creating the pattern may not be correct. Regression analysis of mean bacterial production per cell shows a strong inverse relation with C-DOC and weaker relations with TSS and lake temperature, which are intercorrelated with C-DOC. Positive relations between bacterial production and tempera-

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ture have been well documented (Rae and Vincent 1998; Pomeroy and Wiebe 2001). Conspicuously absent is a significant relationship with NC-DOC, which was what we originally postulated to primarily control bacterial production among the lakes. On the other hand, the significant inverse relation between C-DOC and bacterial productivity does suggest that NC-DOC may be a favoured carbon substrate in this system. Among lakes of the Delta, autotrophic production and macrophyte biomass have been shown to increase with decreasing flood frequency and light attenuation (Squires et al. 2002, 2003). The production of NC-DOC has been coupled with autotrophic biomass in many studies (including this study system; Squires and Lesack 2003*b*). If the NC-DOC is a fully viable substrate, then bacterial production ought to increase with increasing autotrophic biomass unless nutrient limitation becomes a problem (Bird and Kalff 1984; Gurung and Urabe 1999; Jansson et al. 2000).

Reconciling lake patterns of bacterial production with experiments

The nutrient-enrichment experiments seem to demonstrate that nutrient availability is indeed a significant factor in controlling bacterial production among these lakes, but they do not fully support the hypothesis of NC-DOC being a preferred form of carbon substrate. Our nutrient-enrichment experiments were designed to completely eliminate the possibility of nutrient limitation and allow bacterial production to respond solely to the experimental gradient and composition of DOC. The design assumed that differences in the response of bacterial production, following saturation of inorganic nutrients, are due to carbon limitation of one form or another. In the experiment on 31 July 2001, bacterial production per cell clearly increased with increasing NC-DOC, and is consistent with NC-DOC being a fully viable substrate, if sufficient nutrients are available. On the other hand, in the experiment on 17 July 2001, bacterial production per cell responded most strongly under a DOC regime where C-DOC was only modestly higher (Lake 87) than in the lowest C-DOC lake (Lake 280). Taken together, the results from the pair of experiments seem to suggest that both NC-DOC and C-DOC are indeed viable substrates. However, the results also suggest that even though NC-DOC is more abundant in infrequently flooded lakes, bacteria likely can't exploit all of the available substrate in those lakes because they are limited to some degree by shortage of nutrients. Other recent studies have also shown that bacteria can utilize both C-DOC and NC-DOC, with competition within natural bacterial assemblages favouring the species that can best utilize the substrate available (Moran and Hodson 1990; Long and Azam 2001). Differences in bacterial responses among the lakes may also be caused by variation in the bacterial communities produced as a result of the differences in lake flooding frequency and the consequent mixtures of C-DOC and NC-DOC available as substrate. In frequently flooded lakes, the bacterial competition may favour those species capable of utilising C-DOC, whereas the infrequently flooded lakes may favour a community dominated by bacteria capable of rapid turnover of NC-DOC. Phylogenetic information of this type was out with the scope of this project but will be pursued in future investigations.

Reconciling experimental enrichments with nutrient-debt bioassays

Although the nutrient-enrichment experiments seemed to consistently stimulate responses in bacterial production among the lakes, the degree of response was not always consistent with what was expected based on the nutrient-debt bioassays. The size-fractionated N- and P-debt bioassays were designed to partition the uptake, by bacteria, of inorganic nutrients from N and P uptake by the total plankton community. Bioassays were conducted throughout the open-water period among the set of lakes (results will be reported in a separate publication), in addition to the assays conducted at the time of the enrichment experiments. Uptake and release rates of the bacterial (<1 μm) size fraction varied greatly among lakes and over time. The importance of bacteria in regulating nutrients in this study system is illustrated by the observed instances of N and P release. However, when uptake did occur, bacteria seemed to be more limited by P than by N. The highest observed rates of N uptake were not observed in the reported experiments and occurred on 8 August (Spears 2002), accounting for 69% of the total heterotrophic and autotrophic community uptake in South Lake. Bacterial uptake of P accounted for between 3% (South lake, 17 July 2001) and ~100% (Lake 280, both 17 and 31 July) of the total planktonic uptake. These findings confirm that bacteria in lakes of the Mackenzie Delta can indeed act as important sources and sinks of inorganic nutrients and are consistent with similar work in other systems (e.g., Garcia-Ruiz et al. 1999). These results also agree with many recent studies in which bacteria are reported to be limited mainly by P. However, few studies have indicated that N limitation may also be occurring (Cottingham et al. 1997; Carlsson and Caron 2001). Recent studies, including Jochem et al. (2004) and Goldman et al. (1987), generally suggest that the bacterial community can release ammonium and urea from dissolved organic nitrogen.

Constraints on results

There are a few minor constraints on interpreting the results of this paper. The rationale in this investigation for prefiltering water samples to exclude particle-bound bacteria from cell counts was that particle-bound bacteria would have access to alternative sources of nutrients, whereas planktonic cells would only have access to dissolved nutrients. Excluding particle-bound bacteria thus made the interpretation of the nutrient-enrichment experiments more straightforward but may result in cell counts that are not readily comparable with other reported investigations. Another possible reason for lower abundances was that a new DAPI slide preparation procedure used in this study was not fully effective in dispersing the cells and purging humic particles that did pass through GF/C filter. Alternative preparation procedures have been adopted (Febria 2005) that would have yielded higher abundances than obtained here, even after GF/C filtering. The cell counts nevertheless work perfectly well as an abundance index of planktonic (i.e., non-particle-bound) bacteria.

Nutrient-enrichment experiments of the type conducted during this investigation are difficult to set up because the response of per cell bacterial production to nutrient enrichments depends not only on available substrates in the experi-

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mental water, but also on initial density of bacteria. The response parameter of percent increase in per cell production that we used in this investigation ought to account to some extent for differences in the initial densities but may not under all circumstances.

The nutrient-debt bioassays on the bacterial community used in concert with the nutrient-enrichment experiments were historically designed for assessing the nutritional status of phytoplankton, but in the present study, this approach was adapted for bacteria. We acknowledge that physiological studies of the type carried out by Healey and Hendzel (1980) for phytoplankton have yet to be carried out for bacteria as far as we are aware and that the nutrient-debt approach for bacteria should be investigated further. Finally, though steps were taken to minimise the effects of zooplankton grazing of bacteria (filtration through a GF/C filter), it should be noted that some heterotrophic nanoflagellates may pass through a GF/C filter and so our nutrient-debt estimates of uptake and release may not be as accurate as if obtained using pure cultured bacteria.

Significance of results

This study represents the first investigation of which we are aware of the relation between bacterioplankton production and the availability of DOC and nutrients for a system of delta lakes in the circumpolar arctic. Overall, the results of this study show that bacterial production among lakes of the Mackenzie Delta, averaged over the open-water season, mirrors the gradient of T-DOC, ranging from low production in lakes with low T-DOC but high C-DOC to high production in lakes with high T-DOC plus high NC-DOC. The results also indicate that both C-DOC and NC-DOC are viable substrates for the bacterial communities of this system but that limitation of bacterial production by inorganic nutrients is common. We postulate that such limitation is most likely to occur in infrequently flooded lakes with high NC-DOC and high biomasses of macrophytes and epiphytic algae that compete for nutrients but that it may also occur in frequently flooded lakes with high C-DOC after nutrients brought in via river flooding have been depleted. Stimulation of production was observed in all lakes in both nutrient-enrichment experiments. Taken together with N- and P-debt bioassays on the bacterial size fraction, PO_4^{3-} seems to be the most common limiting nutrient for the bacterial community. However, limitation by NH_4^+ may also occur. If the severity of spring ice jams and the consequent magnitude of Mackenzie River flooding declines as a result of climatic warming, nutrient limitation of aquatic bacteria in lakes of the Mackenzie Delta may become enhanced.

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Scale-dependent movements and protection of female blue crabs (*Callinectes sapidus*)

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Abstract: Little is known about the migration of female crabs (*Callinectes sapidus*) to spawning grounds, or how effectively they are protected by North Carolina's "spawning sanctuaries." To investigate migration, we tagged and released a total of 2700 mature female crabs in the fall of 2001 and the summer and fall of 2002 in the three tributaries of Pamlico Sound. Tag returns indicate that females begin migration during September to November and that they probably do not complete it until the next spring. To assess site fidelity and protection of females by spawning sanctuaries, 398 tagged adult females were released in or near sanctuaries at Ocracoke and Hatteras inlets. Most recaptures occurred near the barrier islands (Outer Banks), suggesting that mobility declines once females reach euhaline waters, but recapture data also showed that crabs move over scales larger than sanctuaries and derive only temporary protection by entering sanctuaries. Ovigerous females fitted with ultrasonic pingers were tracked after release inside the boundary of Ocracoke spawning sanctuary. Crabs with orange (new) egg masses meandered over small areas, but those with eggs approaching hatching moved directly seaward. Apparently spawning sanctuaries must be large to be effective; where this is not practical (as in North Carolina), other strategies should be considered.

Résumé : On connaît peu de choses sur la migration des crabes (*Callinectes sapidus*) femelles vers leurs sites de reproduction et sur l'efficacité de la protection que leur fournissent les « sanctuaires de reproduction » de Caroline du Nord. Afin d'étudier la migration, nous avons marqué un total de 2700 crabes femelles matures à l'automne 2001 et à l'été et l'automne 2002 dans les trois tributaires du détroit de Pamlico. La récupération des étiquettes indique que les femelles commencent leur migration de septembre à novembre et qu'elles ne la complètent vraisemblablement pas avant le printemps suivant. Nous avons libéré 398 femelles adultes marquées dans les sanctuaires des baies d'Ocracoke et d'Hatteras ou à proximité afin d'évaluer la fidélité au site et la protection offerte aux femelles par les sanctuaires de reproduction. La plupart des recaptures ont été réalisées près des îles de la barrière (« Outer Banks »), ce qui indique que la mobilité diminue lorsque les femelles atteignent les eaux euhalines, mais les données de recapture montrent aussi que les crabes se déplacent sur des échelles plus grandes que celles des sanctuaires et qu'en entrant dans un sanctuaire, ils ne bénéficient que d'une protection temporaire. Nous avons suivi des femelles ovigères munies d'émetteurs à ultrasons après leur libération dans les limites du sanctuaire de reproduction d'Ocracoke. Les femelles porteuses de masses d'oeufs oranges (nouvelles) errent sur de petites surfaces, mais celles dont les oeufs sont près d'éclore vont directement vers la haute-mer. Il semble donc que pour être efficaces les sanctuaires de reproduction doivent être de grande taille; là où cela n'est pas pratique (comme en Caroline du Nord), il faut envisager d'autres stratégies.

[Traduit par la Rédaction]

Introduction

The purpose of this research was to elucidate the behaviors of female blue crabs (*Callinectes sapidus*) migrating from meso/oligohaline areas throughout the estuarine system, where they undergo their terminal molt to maturity and have their one opportunity to mate, to high-salinity spawning grounds, where they may produce over a dozen broods (Hines et al. 2003) over the next 1–2 years. We also assessed the effectiveness of broodstock protection mechanisms in the largest lagoonal estuary in the US, North Carolina's Albemarle–Pamlico Estuarine System (APES). Commercial harvests of blue crab have declined and remained below historic averages for several years in North Carolina waters (Eggleston 1998; Johnson 2004). Several factors have been invoked, including overfishing of hard crabs (Eggleston 1998; McKenna et al. 1998), increased vulnerability to fishing when freshwater runoff from large storm events concentrates crabs in lower estuaries (demonstrated by dramatic rises in catch-per-unit-effort (CPUE); Eggleston et al. 2004), physical conditions unfavorable for larval and postlarval recruitment (Epifanio and Garvine 2001; Natunewicz and Epifanio 2001; Natunewicz et al. 2001), and mortality associated with cannibalism and interspecific predation (Wilson et al. 1990; Zimmer-Faust et al. 1994; Heck et al. 2001). The broodstock is under increasing pressure; the number of immature females taken for the soft-crab industry is thought to have risen dramatically (Chaves and Eggleston 2003), and many mature females are harvested before reproduction (Uphoff 1998). Because there is a significant stock–recruit relation-

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Fig. 1. The three major oligo/mesohaline subestuaries of North Carolina's Albemarle–Pamlico Estuarine System (APES): Albemarle Sound, Pamlico River, and Neuse River. Numbers correspond to specific geographic locations mentioned in the text: 1, mouth of Core Sound; 2, Jarrett Bay; and 3, Emerald Isle Bridge. Inset shows location of North Carolina in the eastern USA.

ship (Johnson 2004), these trends have sparked interest in broodstock biology and management in the waters of North Carolina and Virginia.

To protect a portion of the blue crab broodstock in the APES based on what was then known of the species' reproductive biology, in 1965 the state of North Carolina set up five "spawning sanctuaries" located at inlets along the Outer Banks and closed them to commercial crabbing from 1 March to 31 August, while continuing to allow the harvest of mature (including ovigerous) females elsewhere. To produce multiple egg masses and release larvae in euhaline water (Millikin and Williams 1984), females must travel seaward after they mate (immediately following their terminal molt to maturity), and it was reasoned that because the five inlets are the only connections between the APES and the coastal ocean, sanctuaries adjacent to inlets would protect a large proportion of reproductive females. Spawning sanctuaries also are being used to manage the broodstock in the lower portions of the Chesapeake Bay, Virginia, and are under consideration in the states of Georgia and South Carolina (S. McKenna, North Carolina Division of Marine Fisheries, 943 Washington Square Mall, Washington, NC 27889, personal communication).

North Carolina's fishery management plan for blue crabs indicates that the protection of the spawning stock is of great concern (McKenna et al. 1998), but the original state documents concerning the establishment and presumed effectiveness of spawning sanctuaries apparently can no longer be found. An assessment of this management tool clearly is overdue and was one goal of our study.

We determined the timing of migration from mating to spawning areas by using mark–recapture techniques. Whether females migrate soon enough after mating to reproduce that same year has important implications for population dynamics because it affects generation time and phasing of larval release relative to cycles of food availability and predation. Rational planning to protect females during migration will require that the routes, as well as the timing, of migration be known.

To assess how adult females use spawning sanctuaries, how effective the sanctuaries are, and how protection of broodstock might be optimized, we also measured movements of females at smaller spatial and temporal scales. In and around the spawning sanctuaries near North Carolina's inlets, we used mark–recapture and also intensively tracked individuals using ultrasonic transmitters.

Materials and methods

Mark–recapture technique: large scale

To study the large-scale movements of adult (mated) females from mating areas to spawning grounds, crabs were individually marked with 2.5 cm × 5.0 cm pink plastic across-the-back tags (Floy Tag, Inc., Seattle, Washington). Releases from mating areas were conducted in the oligo/mesohaline segments of the three major subestuaries of the APES: Albemarle Sound, Pamlico River, and Neuse River (Fig. 1). To study movements of females near spawning grounds and to assess the protection afforded by spawning sanctuaries, releases also were conducted in euhaline waters near Hatteras and Ocracoke inlets (Fig. 2). The tags used in the large-scale mark–recapture studies offered a nominal ($5 US) reward for return of data (date, depth, time, and location of recapture) and bore the phone number and e-mail address of researchers.

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Fig. 2. Location of the five coastal inlets in coastal North Carolina where spawning sanctuaries have been implemented for broodstock management, including the two euhaline release sites where individually marked blue crabs (*Callinectes sapidus*) were released (Ocracoke and Hatteras inlets; black polygons represent sanctuary boundaries).

The large-scale mark–recapture study involved release of 300 postmolt mature female crabs (determined by morphology of their abdomen: triangular when immature, semicircular when adult) in each of the three oligo/mesohaline tributaries at three times for a total of 2700 crabs. It was assumed on the basis of previous studies (Wolcott et al. 2005) that nearly 100% of these females had mated. Healthy, intact crabs were collected in commercial crab pots by collaborating local watermen; the crabs were fitted with tags tied across the dorsal carapace with loops of stainless steel wire around the lateral spines and released in batches at a predetermined location in each tributary over 1–3 days in fall 2001, summer 2002, and fall 2002. The release sites on the western side of Pamlico Sound were in and near the mouths of the Pamlico River (at 35.42351°N, 76.71123°W, in fall 2001; at 35.40028°N, 76.66845°W, in fall 2002) and the Neuse River (at 35.09496°N, 76.60397°W, in fall 2001; at 35.08802°N, 76.55423°W, in summer 2002; and at 35.09333°N, 76.60833°W, in fall 2002) and in the Albemarle Sound close to the mouth of the Scuppernong River (at 36.00000°N, 76.13000°W, in fall 2001; at 35.98434°N, 76.21273°W, in summer 2002 and fall 2002) (Fig. 3). At the initiative of the collaborating crabber, the summer 2002 release in the Pamlico River was performed considerably upstream in Pungo Creek at 35.49867°N, 76.71198°W. Releases began in the Pamlico River on 9 October (fall 2001), 26 June (summer 2002), and 21 October (fall 2002), in the Neuse River on 27 September (fall 2001), 1 July (summer 2002), and 29 September (fall 2002), and in Albemarle Sound on 11 October (fall 2001), 15 August (summer 2002), and 15 October (fall 2002).

For the mark–recapture study of movements in and around spawning sanctuaries, we used euhaline (typically S > 30 psu) release sites on the landward (western) side of the Outer Banks, within or just outside the spawning sanctuaries of Ocracoke and Hatteras inlets (Fig. 2). Mature female blue crabs were captured using commercial crab pots, and those that were healthy and intact were measured, tagged as above, and released immediately. The crab pots used to capture animals at these release sites were being used in a parallel study and were arranged on grids that extended beyond the boundaries of Ocracoke and Hatteras sanctuaries (Fig. 4). A total of 398 individuals were tagged and released from 15 July 2001 to 12 April 2002: 222 at Hatteras Inlet spawning sanctuary (89 inside, 133 outside the sanctuary) and 176 at Ocracoke Inlet spawning sanctuary (99 inside, 77 outside the sanctuary).

For each recapture of a crab, we calculated angle of movement away from the release site, straight-line distance traveled (computed in ArcView 3.2 (ESRI 2002); Hooge and Eichenlaub 1997), speed, and number of days at large. To determine whether movement of animals for each release site, season, and year was directed or random, we applied a Rayleigh's test using the circular statistics program Oriana (versions 1.0 and Beta 2.0; Kovac Computing Services 1994–2003). All angles reported and used in statistical testing are relative to true north. Sanctuary effectiveness was assessed by comparing the proportions of tags returned after crabs were released inside and near sanctuaries with the average proportion of tags returned from crabs released at all of the oligo/mesohaline sites, over all seasons and years.

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Fig. 3. Oligo/mesohaline sites, at each of which 300 individually marked mature female blue crabs (*Callinectes sapidus*) were released en masse in fall 2001, summer 2002, and fall 2002.

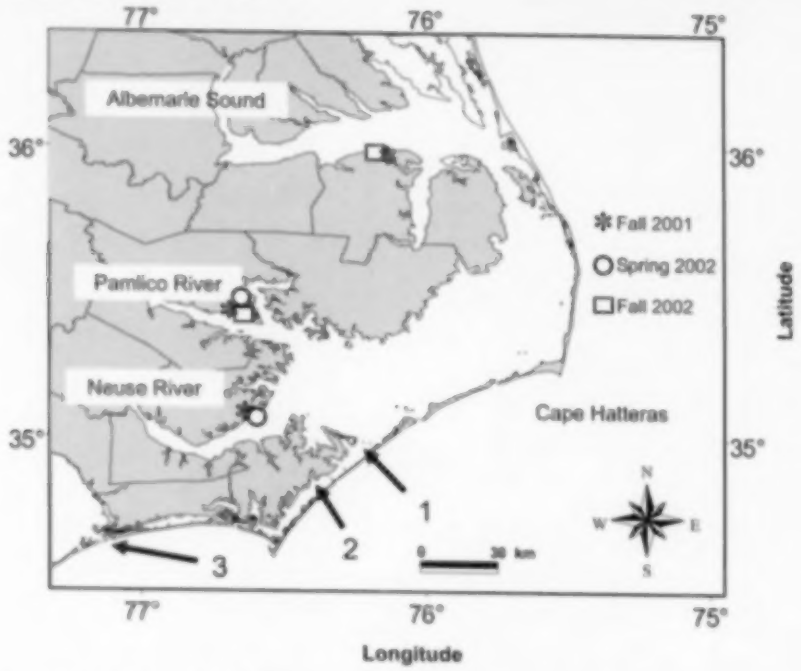
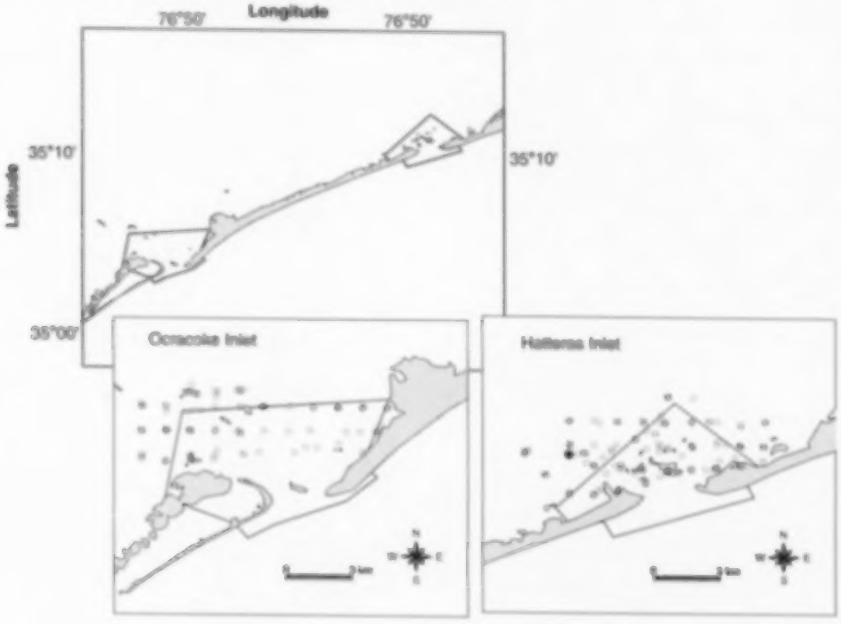


Fig. 4. Euhaline sites where a total of 398 individually tagged mature female blue crabs (*Callinectes sapidus*) were released (open circles represent release sites and lines represent sanctuary boundaries). Collection, tagging, and release were conducted using a grid of pots concurrently being used in a catch-per-unit-effort survey of the sanctuaries.



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To investigate the protection afforded to female crabs released at euhaline release sites relative to sanctuary size, we used ArcView 3.2 (ESRI 2002) to hypothetically extend the boundaries of Ocracoke and Hatteras spawning sanctuaries by 1, 3, 5, and 7 km in all directions. At each incremental increase in the size of the spawning sanctuary, we calculated the number of recaptured crabs that would have been protected by (e.g., contained within) the new, larger sanctuaries.

Tracking of individuals: small scale

To gain insight about microhabitat use and movements at the smaller scale of spawning sanctuaries, egg-bearing females fitted with ultrasonic "pingers" were tracked in and around the spawning sanctuary at Ocracoke Inlet, which at ~45 km^2 is the largest (Fig. 2). Ocracoke Inlet is a typical tidal inlet with many sloughs (small channels), large channels, and shoals and has highly dynamic bathymetry as the result of frequent movement of sediments by tidal and storm-induced currents.

Small-scale tracking of individuals fitted with ultrasonic pingers was conducted during the summer months of 2002 and 2003, times during which sanctuaries are closed to commercial fishing gear. Egg-bearing female blue crabs were captured using commercial crab pots baited and set within the boundary of Ocracoke spawning sanctuary 1–3 days before the start of tracking. Pots were pulled and healthy, intact ovigerous females were measured, fitted with pingers, and released immediately. Intending to elucidate the movements and behaviors of animals throughout the development of a brood, we initially chose females with eggs early in development (recently extruded broods or "orange sponges") for tracking (in 2002, $n = 5$; in 2003, $n = 19$). In most cases, these females were lost (i.e., could not be relocated) before hatching of eggs and release of larvae were expected. To gain insights into behaviors of females with eggs near hatching, we also tracked a few females (1 in 2002; 4 in 2003) with brown or black "sponges" within 4–5 days of hatching and larval release.

An individually coded ultrasonic pinger (75 kHz; designed and built in the Wolcott laboratory) was attached to each crab's dorsal carapace using stainless steel wire or nylon cable ties looped over the lateral spines. A pink across-the-back tag like those used in the large-scale mark–recapture study was also attached to facilitate return of lost animals and transmitters from the commercial fishery.

Females were relocated using an ultrasonic receiver (Sonotronics USR-5; Sonotronics Inc., Tuscon, Arizona) and directional hydrophone that allowed for triangulation to within about 3 m. Positional fixes were obtained from a WAAS-capable GPS receiver (Garmin model 72; Garmin International Inc., Olathe, Kansas).

Crabs were tracked until lost or, in 2002, for a maximum of 6 days because of logistical constraints. For each tagged individual, a position fix (latitude, longitude) was recorded approximately every hour during daylight. At each of the position fixes, we also recorded depth, time, tidal flow (ebb or flood), surface water temperature (2002 only), surface salinity, and depth soundings or transects. To discover any bathymetric features with which animals might be associated, we measured depths with an echo sounder. In 2002, contours at a crab's position were delineated by continuously recording depth along transects 10 m northward, southward, eastward, and westward of the crab's location. During the 2003 field season, a bathymetric map of the entire spawning sanctuary was constructed by taking 2712 soundings as the research vessel drifted or motored along predetermined transects.

To allow for testing of directed movement relative to Ocracoke Inlet, a Rayleigh's test was performed on angles of movement away from the release point, referred to a vector toward the middle of Ocracoke Inlet. Only crabs traveling >150 m were used to explore directed movement, because those moving shorter distances might have simply been meandering while foraging on patchy prey (Hines et al. 1990). Movement vectors for females with early-stage broods were defined by the point of release and the female's last relocation (if at large for less than 8 days) or, if animals were tracked longer, by the last relocation on the 8th day (after which she would have had "late-stage" eggs). Vectors for late-stage females were defined by the release point (for those originally released with late-stage eggs) or the first location on day 9 (for females released with early-stage eggs and tracked longer than 8 days) and the last relocation. Two females released with early-stage eggs were tracked over 14 days; their vectors were terminated on day 14 because spawning would have occurred (Darsono 1992).

Distance between relocations was calculated in ArcView 3.2 (ESRI 2002) using the Animal Movement Extension (Hooge and Eichenlaub 1997). To identify possible environmental cues that animals might use to direct movement or vary speed (wind direction, wind speed, tidal height, and salinity), correlation coefficients (r values) between angle and rate of movement and individual environmental cues were computed. Correlation coefficients are a proxy for the reduction in variance of a variable (e.g., angle of movement) by introduction of a predictor variable (e.g., environmental cue), and correlation coefficients close to 1 or –1 would suggest that the environmental variable in the test is one that the animals could use to direct movement. If blue crabs use environmental cues to direct movement, correlation coefficients between angle or rate of movement and an individual variable averaged across a population would be expected to lie nearer to 1 or –1 than to zero. Because variance in ecological studies is often high, correlation coefficient thresholds of 0.75 to –0.75 were arbitrarily chosen in seeking indications of cues that animals might use to direct movement, accepting a somewhat greater risk of type II error.

We computed correlation coefficients between angle and rate of movement and each of the environmental variables (wind direction, wind speed, tidal height, and salinity) for animals tracked at least 3 days, or those for which we obtained >11 positional fixes. Circular–circular and circular–linear correlation coefficients were provided by Oriana (versions 1.0 and Beta 2.0; Kovac Computing Services 1994–2003), and linear–linear correlation coefficients were provided by Microsoft Excel®. Correlation coefficients for animals tracked during 2002 and 2003 were pooled and averaged (e.g., all correlation coefficients between angle of movement and salinity were averaged across all samples) to test the null hypothesis that r was between 0.75 and –0.75, using a t test. Rejection of the null hypothesis would indicate that movement is correlated with that particular environmental variable and blue crabs are likely to be relying on it

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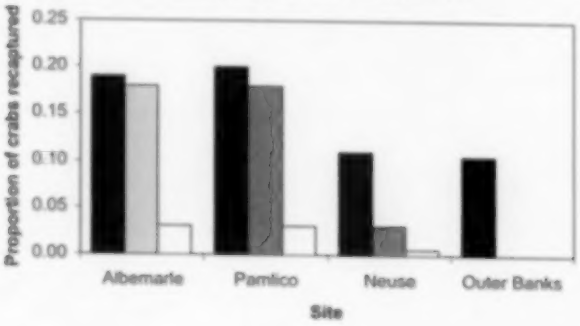
Fig. 5. The proportion of crabs (*Callinectes sapidus*) recaptured by site, season, and year for oligo/mesohaline release sites and the proportion of recaptures (all releases) from euhaline sites (Outer Banks): solid bars, fall 2001 releases; shaded bars, summer 2002 releases; and open bars, fall 2002 releases.



to direct movement and adjust speed. Correlation coefficients, being bounded by 1 and −1, were transformed to meet the *t* test's underlying assumption of unbounded data, using the following equation:

$$(1) \qquad x = \ln((1 + r)/(1 - r))$$

where r is the value of the circular–circular, circular–linear, or linear–linear correlation coefficient, and x is the transformed variable that ranges from ∞ to −∞. For the transformed correlation coefficients (x), a 95% confidence interval (CI) was generated using SigmaStat 3.0 (SPSS Inc. 2003). If the CI overlapped with the range predicted by the null hypothesis, then the result was deemed nonsignificant.

Results

Mark–recapture: large scale

For animals initially released at oligo/mesohaline sites, the proportion reported as recaptured by crabbers was highest for the fall of 2001 release (11% to 20%) and declined with each subsequent release, with the lowest proportion of recaptures (0.3% to 6%) reported for the fall of 2002 (Fig. 5). The proportions of tags recaptured from the Albemarle Sound and Pamlico River release sites were approximately equal and higher for each season and year than the proportion of tags returned from the Neuse River site (Fig. 5).

Tags released at the Albemarle Sound and Pamlico River sites during the falls of 2001 and 2002 were generally recaptured seaward of the release site during the late fall and early winter (Fig. 6). Animals released from the Albemarle Sound and Pamlico River during the summer of 2002 did not move substantial distances seaward until late September or October–November (Fig. 6). Animals released at the Neuse River site during the fall of 2001 were recaptured seaward of the release site during the late fall – early winter, whereas the few tags returned from the summer 2002 and fall 2002 releases tended to be from near the site of initial release (Fig. 6).

Movement of female crabs was oriented from mating areas toward spawning grounds (i.e., generally toward the nearest inlet). In applying Rayleigh's tests to recaptures from all

Fig. 6. Recaptures of adult female *Callinectes sapidus* from oligo/mesohaline release sites (Albemarle Sound, Pamlico River, and Neuse River) by season and year: (*a*) fall 2001, (*b*) summer 2002, and (*c*) fall 2002. "RS" represents release site. Each dot represents one recapture; beside each symbol in the legend is number of days at large that symbol represents. To allow distinguishing river of origin, symbols for the Pamlico (middle tributary) data are shaded. All unshaded symbols to the north are from Albemarle Sound crabs, and all unshaded symbols to the south are from Neuse River crabs.

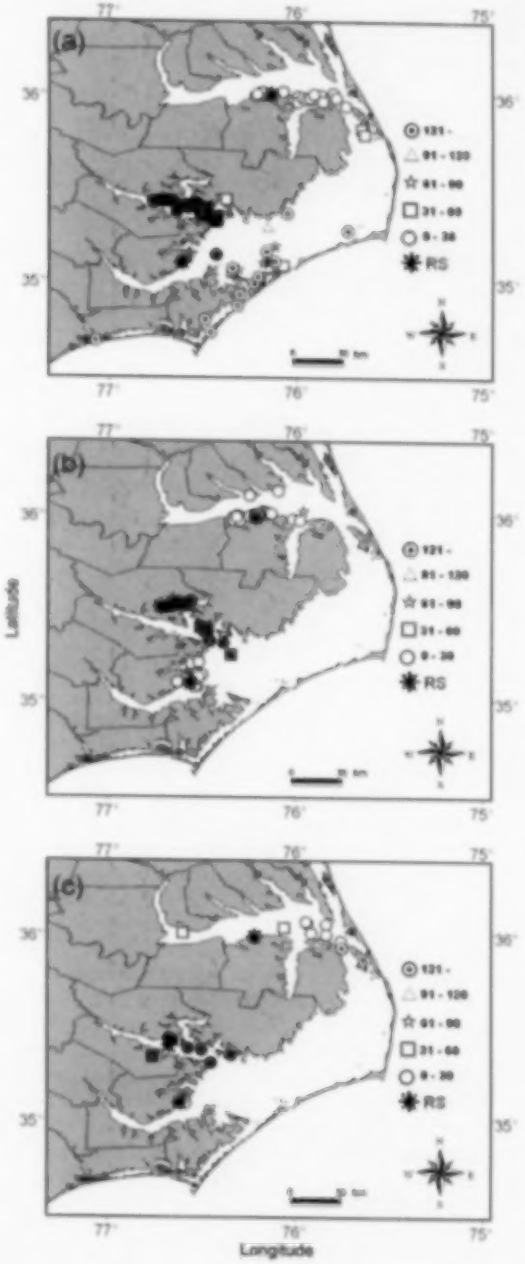


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Table 1. Movement of female blue crabs (*Callinectes sapidus*) in large-scale mark–recapture.

Site and season	No. of observations	Mean vector (μ) (degrees (°) true)	Circular variance	Circular standard deviation (degrees (°))	95% confidence interval for mean vector (degrees (°) either side of μ)	Rayleigh test (*Z*)	Rayleigh test (*p*)
Neuse River							
Fall 2001	33	105.24	0.142	31.672	10.771	24.311	<0.001*
Summer 2002	9	42.78	0.550	72.080	108.130	1.844	0.16
Fall 2002	2	97.59	0.003	4.602	20.175	1.987	0.14
Pamlico River							
Fall 2001	58	100.39	0.242	42.634	10.862	33.340	<0.001*
Summer 2002	55	90.65	0.037	15.630	4.131	51.056	<0.001*
Fall 2002	10	61.82	0.517	69.120	53.312	2.333	0.095*
Albemarle Sound							
Fall 2001	57	249.59	0.656	83.654	29.594	6.762	<0.001*
Summer 2002	55	14.11	0.820	106.188	120.834	1.773	0.17
Fall 2002	9	82.26	0.231	41.509	32.210	5.325	<0.001*
Fall 2002 (after 31 October)	20	105.12	0.153	33.054	14.422	14.338	<0.001*

Note: Movements were significantly directional by Rayleigh's test (asterisk (*) denotes $p < 0.1$) for all sites, seasons, and years except Neuse summer 2002, Neuse fall 2002, and Albemarle summer 2002. In each case showing significant directionality by Rayleigh's test, mean directions were seaward except that of Albemarle Sound fall 2001. Crabs from the Albemarle Sound fall 2001 release began to exhibit significant seaward directionality only after 31 October 2001.

release sites, seasons, and years, we elected to use an alpha level of 0.1 because of the inherent variability of animal movement data. By this criterion, all results were significant except those for the Neuse River releases in the summer of 2002 ($p = 0.16$) and fall of 2002 ($p = 0.14$) and the Albemarle Sound release in the summer 2002 ($p = 0.17$). For most releases that showed significant directionality, the mean direction was seaward and towards the closest inlet (i.e., for Neuse River and Pamlico River, Hatteras and Ocracoke inlets; for Albemarle Sound, Oregon Inlet). The exception was the Albemarle Sound fall 2001 release (mean angle = 249.59°, away from inlets). However, when this test was repeated for the Albemarle Sound fall 2001 release using only those crabs recaptured on or after 15 October 2001, there was a significant ($p < 0.001$) mean angle seaward (105.12°) (Table 1).

Crabs tagged in the western tributaries of Pamlico Sound typically moved several kilometres per day, up to a maximum of 7 km·day^{-1}. The distance they covered was a function of how long they remained at large, generally 1–3 weeks, although some were caught on the day of release and a few escaped the fishery for a few months to over a year. Among crabs released at oligo/mesohaline sites for all seasons and years, those released in the Neuse River in fall 2001 traveled the farthest. Individuals were recaptured south of Pamlico Sound near Drum Inlet (approximate distance of 74.8 km), the Emerald Isle Bridge (approximate distance of 134.0 km) (Fig. 1), and Wrightsville Beach (approximate distance of 223.4 km).

Nine animals that were initially released at oligo/mesohaline sites were recaptured twice by the commercial fishery and yielded additional information about movements. Of these, seven were recaptured seaward of their initial release site, re-released, and later caught farther seaward. The two remaining individuals were unique. One, initially released at the Neuse River site and at large for 173 days, was recaptured seaward of the release site, near the mouth of Core Sound (Fig. 1). It was re-released and recaptured a second time west of Drum Inlet near Jarrett Bay (Fig. 1). The second animal, initially released in the Albemarle Sound and at large for 107 days, was first recaptured in Pamlico Sound near the mouth of a canal connecting it with the Albemarle via Lake Mattamuskeet, re-released, and subsequently recaptured farther east in Pamlico Sound. Movement of this animal implies that some crabs may use the intracoastal waterway (ICW) as a corridor between tributaries.

The location where crabs were released had little effect on the probability of recapture. The proportion of tags returned from crabs that were initially released in euhaline waters (in or near sanctuaries) at the Outer Banks was virtually the same as that from crabs released at oligo/mesohaline sites (Fig. 7), and the proportion of tag returns from animals initially released in or near the Hatteras spawning sanctuary was scarcely higher (11.26%) than that from animals released in or near the Ocracoke spawning sanctuary (9.66%). It appeared that the degree of protection accruing to crabs released near the sanctuaries, or even inside them, was inconsequential; recapture rates were almost identical to those of crabs released on the western side of Pamlico Sound (Fig. 8). Had the Hatteras and Ocracoke spawning sanctuaries been larger in the years of this study, each incremental expansion would have made them more effective (Table 2), but protecting more than half of the crabs would have required doubling their dimensions (roughly quadrupling their area). This calculation relies on the assumption that respect for and enforcement of sanctuary boundaries would not change if sanctuaries were expanded, and we emphasize that this only estimates incremental protection of females that had already reached euhaline waters, not that of the presumably much larger contingent still en route.

Animals released at euhaline sites, with few exceptions, remained in euhaline waters and were recaptured near the Outer Banks (Fig. 9). Two were recaptured twice. The first recapture in both instances was by the commercial fisher

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Table 2. Incremental protection that enlarged sanctuaries would have provided female crabs (*Callinectes sapidus*) released at euhaline sites (in or near Ocracoke and Hatteras spawning sanctuaries) and recaptured by the commercial fishery.

Expansion of sanctuary boundaries (km in all directions)	No. of additional crabs protected			Percent crabs protected
	Ocracoke	Hatteras	Total	
1	1	1	2	5
3	6	14	20	49
5	10	18	28	68
7	11	22	33	80

Note: Number of additional females that would have been protected by each expansion of the sanctuaries' boundaries in all directions, and the proportion of the total that would have been protected, are shown.

Fig. 7. The average proportion of crabs (*Callinectes sapidus*) recaptured from oligo/mesohaline release sites (averaged across seasons and years) compared with the proportion recaptured from the euhaline release sites (Outer Banks). The numbers above each bar represent the total number of animals released at each site.

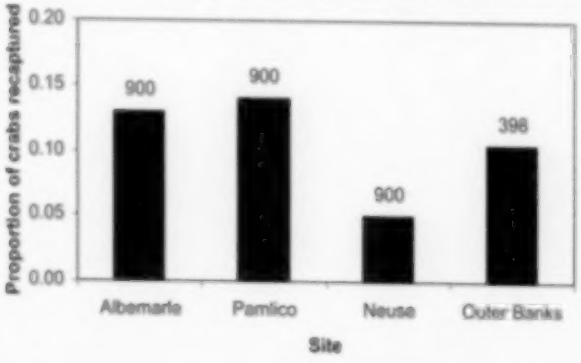
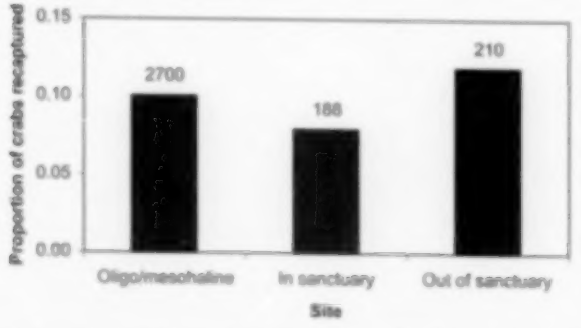
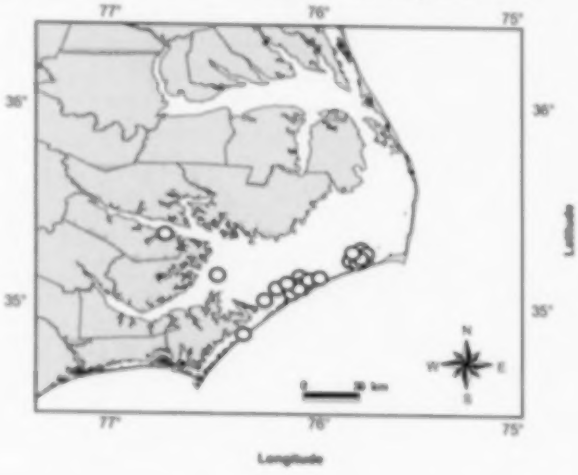


Fig. 8. The proportion of crabs (*Callinectes sapidus*) recaptured that were initially released inside or outside the boundary of Ocracoke and Hatteras spawning sanctuaries compared with the proportion of all tags recaptured from oligo/mesohaline sites. The numbers above each bar represent the total number of animals released at each site.



who was contracted to tag and release animals, and the second recapture was by another commercial crabber. One animal, initially released at Ocracoke, was first recaptured within 100 m of where it was initially tagged and recaptured a second time 31 km away, just north of Hatteras spawning sanctuary, after 39 days at large. The second animal, initially released at Hatteras, was first recaptured within 1.5 km of its initial release site and then caught again, still within 5.5 km of Hatteras Inlet, after 15 days at large.

Fig. 9. Recapture locations (open circles) of individually marked mature female crabs (*Callinectes sapidus*) released from euhaline sites in or near Ocracoke and Hatteras spawning sanctuaries.



Tracking of individuals: small scale

Adult female crabs fitted with ultrasonic pingers and released in the Ocracoke sanctuary remained within its boundaries as long as they could be followed. In the 2002 field season, six females were tracked intensively for 1–6 days (average 3.2 days), and all relocations were inside the spawning sanctuary. Three females with early-stage eggs were tracked for more than 2 days. None of these females was returned by the commercial fishery. Despite the small sample size, patterns of movement and microhabitat selection were evident: females tended to move seaward during the evening and night hours, showed low mobility during daylight hours, tended to stay on the edges of sloughs and channels rather than the deepest or shallowest portions of the sanctuary, and showed no preferred habitat but were tracked into all sediment types (sand and mud) at varying proximity to seagrass beds.

Similar patterns were seen during the 2003 field season when 23 females were fitted with pingers, released, and intensively tracked within the boundary of Ocracoke spawning sanctuary. Fourteen females with early-stage eggs were

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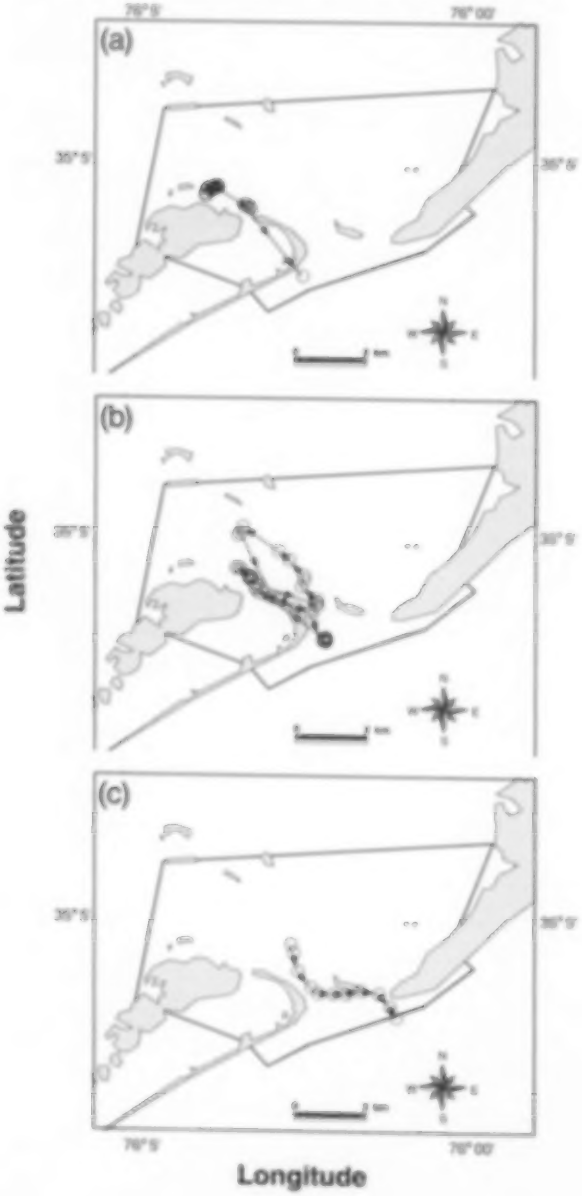
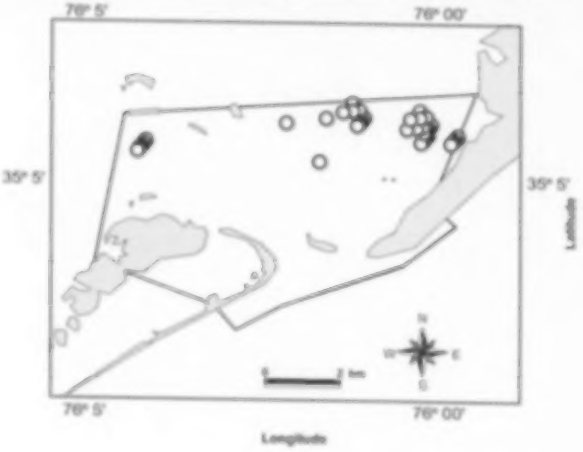
Fig. 10. Movement of ultrasonically tracked egg-bearing female *Callinectes sapidus* captured, tagged, and released within the boundary of the Ocracoke spawning sanctuary (polygon): (*a*) female with early-stage egg mass tracked during the summer of 2002 for 6 days; (*b*) female with early-stage egg mass tracked during the summer of 2003 for 27 days; (*c*) female with late-stage egg mass tracked during the summer of 2003 for 1 day.



tracked 3 days or longer, and four with late-stage egg masses were tracked for 1–2 days. Again, all relocations of these crabs were inside the boundary of the Ocracoke spawning sanctuary. The crabs remained at large for 1–27 days, averaging 7.6 days. Seventeen percent of pingers lost to tracking

Fig. 11. Positions (from global positioning system) of illegal crab pot buoys (open circles) found on six different days within the boundary of the Ocracoke spawning sanctuary (outlined).



were returned by the commercial fishery, three from outside the boundary of the spawning sanctuary and one from inside it. One crab recaptured by the commercial fishery 35 days after initial release had a late-stage egg mass. This presumably was a different brood than the one she was carrying when tagged; that one would have hatched within ~14 days. As in 2002, brooding females showed no preference for any habitat type and were tracked into sand and mud habitats at various proximities to eelgrass beds. In contrast to 2002, though, in 2003 crabs were tracked into the deepest (11 m) and shallowest portions (0.5 m) of the sanctuary and moved during the day, as well as at night.

Females with early-stage eggs tended to move slowly and without pattern, but as the brood developed, they began to move at higher rates and generally seaward (Fig. 10). Early in brooding they meandered slowly (0.048 km·h^{-1} or 1.1 km·day^{-1}) without significant directionality by Rayleigh's test ($n = 23$, $p = 0.417$). Those with late-stage eggs showed rapid (0.394 km·h^{-1} or 9 km·day^{-1}) movement, significantly directional by Rayleigh's test ($n = 7$, $p = 0.033$), toward the inlet.

None of the environmental variables tested as potential cues was significantly correlated with angle and (or) rate of movement. An additional variable that we had not planned to measure but which influences the effectiveness of spawning sanctuaries is the degree to which they reduce fishing pressure. During the entire 2003 tracking study, illegal crab pots were seen within Ocracoke spawning sanctuary. To quantify their abundance, positions of 124 illegal pots were plotted on six different days using a GPS receiver (Fig. 11). Initially they were densest in the peripheral areas of the sanctuary, but as poaching approached its peak in the 3rd week of July, they extended well into the interior.

Discussion

Once female blue crabs have undergone their terminal molt to maturity and mated in oligo/mesohaline zones of estuaries, they must migrate seaward to where salinities are

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high enough for larval development. The timing of migration relative to cycles of food availability and water temperature has far-reaching consequences. The distance of migration can vary from tens (APES) to hundreds of kilometres (Chesapeake and Delaware bays). Migration to these areas presumably requires substantial energy provisions, certainly for locomotion and probably for physiological adjustments as well. Costs of migration for marine invertebrates have received little attention, although they have been studied in birds, insects, and salmon (Johnson 1969; Aidley 1981; Gwinner 1990).

Female blue crabs starting a spawning migration have (at least) two options: (*i*) migrate immediately to spawning grounds right after mating and begin releasing larvae that same year, or (*ii*) delay migration while building up muscle and energy reserves for use in subsequent migration and brood production. These two options for the timing of migration present ecological trade-offs. Knowledge of the timing and route of migration also will be essential in formulating rational policies for protection of the broodstock during the migratory phase.

Females that migrate right after mating would have a good chance of hatching at least one brood before the winter months, thereby increasing their potential fitness by shortening generation time. On the other hand, energy stores of females that have just molted to maturity and mated are at a minimum relative to body size (Turner et al. 2003) and must be used to grow tissue to fill and operate the new, substantially larger, exoskeleton. It seems unlikely that these stores would be sufficient to also fuel migration all the way to the spawning grounds; to support locomotory costs they would almost certainly need to be augmented through feeding along the migration route, and to support brood production they would require a large build-up through intensive foraging after arrival on the spawning grounds. Foraging does occur during migration, confirmed directly by biotelemetry (Turner et al. 2003; T.G. Wolcott and D.L. Wolcott, unpublished data) and indirectly by the strategy of commercial crabbers, who believe migrating females are "hungry" and target them (successfully) using baited pots.

Females delaying migration until the fall months would have time to build up energy reserves before migration. Recently molted blue crabs in the Chesapeake Bay allocate energy sequentially (Turner et al. 2003), as might be expected (Adiyodi 1985), first into new muscle tissue (needed for migratory locomotion, foraging, and defense) and then into the ovaries and the storage deposits (hepatopancreas) needed first for migration down the bay and eventually for brood production once at the spawning grounds. These late-migrating females would have a low probability of reaching the spawning grounds in time to hatch brood(s) before the end of the warm reproductive season, and any broods they did produce might have low survival because of low food supply for larvae during cold months. Late-migrating females also would have a longer generation time, hence lower r and population growth rate, than those that migrate promptly after mating (assuming no change in duration of other life history stages).

Anecdotal information from commercial and recreational fishers in Pamlico Sound suggests that female blue crabs, which could have mated any time since waters warmed in spring, start their migration toward spawning grounds only in late September – early October. This is what has been found in Chesapeake Bay, using ultrasonic pingers (Turner et al. 2003) and conventional mark–recapture techniques (Aguilar et al. 2005). In Pamlico Sound, North Carolina, trawl surveys in June, August, and September of 2002 showed no seaward movement of the centroid of the adult female population (Eggleston et al. 2004). Had such a shift been evident, it could have been attributed to sequential depletion of local populations beginning up the estuary in the tributaries or by seaward migration of individuals; the data indicate that neither was occurring during that summer (a low-runoff year). Crabbers are sufficiently convinced of a September onset of migration that in late fall they move their pots progressively seaward to follow the "pulse" of migrating crabs.

Tag returns from our large-scale mark–recapture study are consistent with the anecdotal information from fishers; most females remain in oligo/mesohaline waters through the summer and migrate toward spawning grounds during the fall months. Females beginning migration in September–October have the potential of reaching spawning grounds in the year of insemination (average speed of fall-released animals = 0.842 km·day^{-1}), although the majority of them probably overwinter somewhere in the estuary, perhaps near the Outer Banks. The spawning migration is not completed (i.e., larvae are not spawned) until the spring months following the year of insemination. This is evident from oligo/mesohaline-released animals not being recaptured on euhaline spawning grounds until after the first of the year.

Our inference that most females do not migrate until late summer – early fall is consistent with the observations of earlier workers. In a large-scale mark–recapture study from 1957 to 1965 in the waters of North Carolina (Judy and Dudley 1970), 22 928 adult blue crabs (17 237 females) were individually tagged and released (no specific dates given) and 5205 females were recaptured by the commercial fishery. During April–June, most animals were recaptured near the site of release or in the coastal ocean and were thought to be females moving from estuaries to the coastal ocean to spawn larvae. We suggest that these recaptures reflected females that completed their spawning migration and began to release larvae in the spring. They had not reached spawning grounds in the previous year during which they were inseminated, and had overwintered in estuarine waters near the Outer Banks. This is consistent with observations from Chesapeake Bay, where tracking of crabs with ultrasonic pingers (Turner et al. 2003) and conventional mark–recapture studies (Aguilar et al. 2005) all indicate that females typically remain all summer near where they mated and begin migrating seaward in the fall.

It has been suggested that the spawning migration within the APES begins in the spring months (Johnson 2004), based on a minor peak in postlarval settlement being recorded in the spring at Oregon Inlet and a major peak in the late summer – early fall. This interpretation is problematic for several reasons, especially because the minimum latency between mating and extrusion of the first brood is about 14 weeks (Wolcott et al. 2005). The spring peak of larval settlement can only be coming from females that mated and

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migrated in the previous summer and fall and hence were already on the spawning grounds when waters warmed in the spring. Furthermore, back-calculations based on estimated duration of larval life are risky. Recruitment into estuaries is highly dependent on hydrodynamic and environmental processes (Garvine et al. 1997; Epifanio and Garvine 2001), and larval abundance and settlement is patchy in time and space (Garvine et al. 1997; Natunewicz and Epifanio 2001; Natunewicz et al. 2001). The duration (mean number of days and variance) of the postlarval stage in nature is not well understood. Observed peaks in settlement may be the consequence of larval delivery, rather than of larval production. The situation is further complicated by the possibility that postlarvae appearing at Oregon Inlet could be supplied by other estuaries (i.e., Chesapeake and Delaware bays). We will be able to confidently relate larval settlement data to the condition of the North Carolina spawning stock only when we know more about the spawning behavior and biology of female crabs resident on spawning grounds and about the time course of larval development in the coastal ocean.

At the smaller scale of the spawning sanctuaries themselves, our tag return data and tracks of individuals with ultrasonic pingers show that once adult females reach euhaline waters, they move much less than females tagged before migration (but still on scales much larger than the North Carolina sanctuaries). Our data gave no indication that there were microhabitat types preferentially used by mature females or sponge crabs that therefore should be specifically included in spawning sanctuaries.

Recaptures of our tags and our tracking of mature females released in euhaline waters (in or near spawning sanctuaries) confirm that sanctuaries will protect some proportion of females. Once they reach high salinities, most females stay close to spawning grounds and do not migrate back up the estuary; few tag recaptures occurred far from the Outer Banks. This is consistent with how we expect natural selection to have operated in these estuarine systems. It would favor conserving energy reserves that could be put into brood production and predator avoidance. Only if areas in and around spawning grounds were depleted of forage or presented high risk of predation would crabs be expected to spend energy migrating back up the estuary. Food depletion near inlets does not appear to be the case; areas along the Outer Banks in the vicinity of spawning grounds have extensive seagrass beds that support high densities of benthic prey, including hard clams (*Mercenaria mercenaria*), abundant enough to support a recreational fishery. Risk of predation may be higher for adult female crabs near inlets because of the potentially higher encounter rates with potential predators. Large fish and sea turtles do eat adult blue crabs, crabs are commonly used as bait by angling surf fishers, and turtles often destroy crab pots to forage on crabs and bait. However, the numbers of crabs taken apparently are not large, and predation does not seem to be a strong enough selective force for animals to migrate back up the estuary between broods.

Our tracks of ovigerous females are consistent with a conceptual model based on in situ observations of females using selective tidal stream transport (Tankersley et al. 1998) and work from previous studies (Tagatz 1968; Millikin and Williams 1984). Females with early-stage eggs move randomly and exhibit low mobility, which we interpret as searching for forage without straying far up the estuary. When eggs develop to within a few days of hatching, females direct movement seaward, which is thought to facilitate the export of larvae to the coastal ocean where their survival is maximized.

Although we found no significant correlation between any environmental variable and angle or rate of movement, we cannot reject the hypothesis that female crabs use environmental cues to direct movement. The bathymetry of the Ocracoke spawning sanctuary is complicated by sloughs, channels, and shoals. These features influence water movements, causing unknown lags and increased variance in the times at which environmental cues reach animals at different sites. Significant correlations may exist but remain undetectable without additional data.

To be effective, management strategies must safeguard a sufficient proportion of the broodstock, both egg-bearing and non-egg-bearing females, as the reproductive potential of each is similar in a species that produces multiple broods. The intent of the North Carolina spawning sanctuaries was to encompass an area large enough to protect the bulk of the spawning stock without disproportionately disadvantaging the Outer Banks commercial crabbers, who rely almost entirely on catching females, but they fail to accomplish this objective because they are too small. Females can begin producing broods far outside boundaries of the spawning sanctuaries or can wander there while carrying broods. They move so quickly (1–9 km·day^{-1} in this study) that during the approximately 2 weeks from egg extrusion to hatching they could move 14–126 km, far enough to easily walk from the middle of Pamlico Sound to its edges. Indeed, ovigerous females are taken occasionally by the regular North Carolina Division of Marine Fisheries trawl surveys in Pamlico Sound; since 1987 they typically have appeared within a 14 km radius of Ocracoke Inlet, or nearly halfway across Pamlico Sound (S. McKenna, North Carolina Division of Marine Fisheries, 943 Washington Square Mall, Washington, NC 27889, personal communication). Given the females' mobility, it is not surprising that many females released inside sanctuaries in our study "diffused" out and became available for legal harvest. Females gain only temporary protection by entering a spawning sanctuary; we emphasize that the probability of eventual capture is about the same for those released inside or anywhere outside of sanctuaries.

Protection of more than half of the euhaline-released females in our study would have occurred only if the sanctuary dimensions had been nearly doubled to about a 14 km radius of the inlets. Larger sanctuaries with fixed boundaries might not even provide adequate protection in all years. Anecdotal information from crabbers, as well as CPUE data (Eggleston et al. 2004), suggest that distribution of females is strongly influenced by the amount of freshwater input to the APES. The commercial crabber who collaborated in this study, Mr. Eugene Ballance of Ocracoke, North Carolina, has found over many years that during flood years, females are caught almost exclusively along the Outer Banks, whereas during drought years, they are harvested throughout Pamlico Sound. In his opinion, the low effectiveness of the Ocracoke sanctuary during the low-runoff years of our study was attributable at least in part to females ranging farther up the

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estuary with the high salinities. An ideal spawning sanctuary would require boundaries that expand landward in drought years and along the shore into adjacent euhaline areas near the Outer Banks in flood years, but this probably would be impractical.

To be effective, a sanctuary needs to be not only large enough, but also effectively enforced. Enforcement even of the present small sanctuaries with fixed boundaries can tax the resources of the marine police. Illegally placed pots were seen inside the boundary of Ocracoke spawning sanctuary during all months of the 2003 tracking study, but only once was a state enforcement officer observed checking them. The remoteness of Ocracoke and other sanctuaries makes maintaining a regulatory presence, and discouraging poaching, costly. If spawning sanctuaries were expanded to close more of the traditional crabbing areas and if their boundaries varied from year to year (requiring revised boundary marking systems and public notices), we suspect that the incidence of poaching would only increase.

Sanctuaries of appropriate size do seem to be effective. The sanctuary in the lower reaches of Chesapeake Bay encompasses ~440 km^2, an area larger than the movements of the ovigerous females we tracked, and presumably protects most of the broodstock once females reach the spawning grounds (although they are vulnerable to the winter dredge fishery). Because most estuarine systems along the east coast of the US are small (especially those of Georgia and South Carolina, the states currently considering spawning sanctuaries as management strategies), possible alternatives to spawning sanctuaries should be considered.

Among these is a partial or total ban on the harvest of females (egg-bearing and (or) non-egg-bearing), which would ensure that the broodstock is protected but could have a disproportionate impact on and engender political turmoil from some regions. On the Outer Banks of North Carolina, crabbing for females once was a major industry, although it has been supplanted by tourism as the primary economic driver. Advantages to banning the take of females are that it would increase the number of individuals contributing larvae and possibly increase the number of recruits re-entering the estuarine system.

Size restrictions on females should also be considered as an alternative management strategy. There are two goals that need to be considered: maximizing larval supply and minimizing the probability of genetic selection for small size at maturity. Different strategies may be required to meet each. The first would be achieved by protecting a subset of the broodstock that is likely to produce, at short intervals, broods that are numerous and (or) large. Adjusting the lower size limits for females has been considered irrelevant because juvenile females are almost invariably below the lower legal size limit for male hard crabs, whereas most adult females are above it. Females, with few exceptions, have a terminal ecdysis; unlike undersized males, they would never grow any larger and subsequently recruit to a fishery with a larger minimum legal size. However, raising the minimum legal size for hard females, or increasing the size of cull rings in pots, would protect the smaller adult females. These size classes, by virtue of producing broods at shorter intervals than the largest females, have roughly equivalent reproductive potential (G.H. Dickinson, D. Rittschof, and C. Latanich, Duke University Marine Laboratory, 135 Duke Marine Lab Road, Beaufort, NC 28516, USA, unpublished data). They have low market value and typically are sent to packinghouses, so protecting them would have relatively low economic impact on crabbers.

The other goal, avoiding genetic selection for small size at maturity, is relevant to the fishery because the largest crabs (but especially males) always command the highest prices. Protecting the smaller females would ipso facto impose selective advantage for maturing at small size (see below also). Protecting the largest females by setting an upper size limit (a strategy employed for some fin fishes; a 171 mm upper limit now is proposed for the North Carolina hard-crab fishery) would still allow harvest of many females but allow the presumably most fecund individuals to escape. If females above a maximum legal size were protected regionally to overcome effects of larval mixing offshore, it would (if control of size at maturity has a substantial genetic component) also favor genetic diversity and potentially reverse the historical decrease in average size of crabs in the population. There is evidence that the proportion of dwarf females (ones that become reproductive at <100 mm carapace width) is increasing (Johnson 2004). Dwarf females can continue producing broods without mortality from the commercial fishery because they can escape crab pots through cull rings or even through the openings of the wire mesh. The selection this imposes (again assuming that size at maturity has a substantial genetic component) could have far-reaching implications, including a shift toward smaller sizes in females of succeeding generations (Conover and Munch 2002), a decrease in the size of broods produced, and perhaps reduced mating success or selection for smaller size at maturity of males, too, if dwarf females cannot mate with normal-sized males. An upper legal size limit would favor reproduction by larger individuals and counter the fishery's strong selection pressure. These big females would contribute larvae (and genes) to the next generation over the next year or more, which argues for a year-round embargo rather than a seasonal (winter) closure as proposed for North Carolina. Enforcement of an upper size limit would be difficult for the recreational fishery (the impact of which is poorly understood) but simple for the commercial fishery. Presently, enforcement is focused at the crab houses, where no more than 5% of the crabs bought can be of illegal size. An upper size limit would need to be set to protect a sufficiently large proportion of the female population; in much of Pamlico Sound, only 1% of the females are above the upper size limit proposed for North Carolina, and the 5% tolerance would render the regulation meaningless. Incremental mortality from a catch-and-release scheme probably is not a concern; crabs collected in pots and subsequently held 1–2 weeks in laboratory tanks showed survival >87% (T. Ziegler, Duke University Marine Laboratory, 135 Duke Marine Lab Road, Beaufort, NC 28516, personal communication), and those returned immediately to the water probably would survive even better.

There might be impacts on other sectors of the fishery if take of females is reduced. Females are caught mostly near the Outer Banks, but many crabbers around Pamlico Sound now have fast boats and work pots in parts of the estuary distant from their home ports. Excluding large females from

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the fishery might shift additional fishing pressure onto males in the upper estuary. Even if this occurred, despite all the circumstantial evidence leading us to expect sperm limitation where males are heavily fished (Hines et al. 2003), it seems unlikely to become a problem, at least within the estuaries. Virtually all females sampled throughout North Carolina waters had mated and still had enough sperm for at least one additional brood (Wolcott et al. 2005; D.L. Wolcott, unpublished data). Given crabbers' mobility, there would probably not be a disproportionate impact on Outer Banks crabbers, who traditionally have been the ones relying on females.

In summary, female blue crabs migrate fairly synchronously from mating areas to spawning grounds during the late fall – early winter in North Carolina waters and the upper reaches of the Chesapeake Bay (Turner et al. 2003; Aguilar et al. 2005), regardless of when they mate. Although many crabs could reach spawning grounds in the year of insemination if they migrated promptly after mating, the majority that begin migration in September–October must arrive after the end of the reproductive season. Many probably overwinter in estuaries part way to the spawning grounds and do not complete migration (i.e., begin brooding) until the spring months of the year following insemination. Once on spawning grounds, females stay near the Outer Banks, without clear microhabitat preferences and without migrating back up the estuary. Brooding females with early-stage eggs show low mobility and meander, whereas those with late-stage eggs show seaward-oriented movement.

Females move over scales larger than the North Carolina spawning sanctuaries, and their probability of being caught by the fishery is about the same whether they are tagged on the west side of Pamlico Sound, or near a spawning sanctuary, or inside the sanctuary boundary. Large spawning sanctuaries like that in Chesapeake Bay seem to be effective, whereas small ones seem to provide minimal protection to the spawning stock. Agencies currently using or considering small-scale spawning sanctuaries should explore alternative management strategies, including a total or partial ban in time and space on the harvest of females and imposition of an upper size limit for taking mature females.

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Continued disappearance of the benthic amphipod *Diporeia* spp. in Lake Michigan: is there evidence for food limitation?

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Abstract: Benthic surveys were conducted in the southern basin of Lake Michigan and throughout the lake to assess trends in benthic populations, emphasizing recent changes in densities of the benthic amphipod *Diporeia* spp. and dreissenid mussels. In the southern basin, *Diporeia* populations declined 89%, 91%, and 45% between 1993 and 2002 at sites <30, 31–50, and 51–90 m, respectively. Lakewide, the population declined 65% between 1994–1995 and 2000. Over the same time period, dreissenid densities, particularly *Dreissena bugensis*, increased. Intensive studies at 45 m sites in the southeastern region examined changes in lipid content, age structure, and benthic food inputs relative to the hypothesis that food limitation was a factor in *Diporeia*'s disappearance. As *Diporeia* densities declined to zero, length–weight remained unchanged, and lipid content generally increased. Recruitment still occurred, but the young did not survive to become adults. Based on organic carbon, biogenic silica, and chlorophyll collected in sediment traps and found in the upper sediments, pelagic inputs to the benthic region still occurred. Our field observations and laboratory experiments did not disprove the hypothesis that food limitation from dreissenid filtering activities was the cause of the decline, but direct relationships between the loss of *Diporeia* and indicators of food availability were difficult to establish.

Résumé : Nous avons inventorié le benthos dans le bassin sud du lac Michigan ainsi que dans le lac dans son ensemble afin de déterminer les tendances dans les populations benthiques, en particulier les changements récents de densité de l'amphipode benthique *Diporeia* spp. et des bivalves dreissénidés. Dans le bassin sud de 1993 à 2002, les populations de *Diporeia* ont diminué respectivement de 89 %, 91 % et 45 % dans les sites situés à <30, 31–50 et 51–90 m, respectivement. À l'échelle du lac, les populations ont diminué de 65 % entre 1994–1995 et 2000. Durant la même période, les densités des dreissénidés, particulièrement de *Dreissena bugensis*, ont augmenté. Des études poussées aux sites de 45 m ont évalué les changements du contenu lipidique, de la structure d'âge et des apports de nourriture benthique en relation avec l'hypothèse voulant que la carence de nourriture soit un facteur dans la disparition de *Diporeia*. Au moment où les densités de *Diporeia* déclinaient vers zéro, la relation longueur–masse est restée inchangée et le contenu lipidique a en général augmenté. Il y avait encore du recrutement, mais les jeunes ne survivaient pas jusqu'à l'âge adulte. D'après les mesures de carbone organique, de silice biogénique et de chlorophylle effectuées dans les pièges à sédiments et dans les sédiments superficiels, il y avait encore des apports pélagiques vers la région benthique. Nos observations de terrain et nos expériences de laboratoire ne permettent pas de rejeter l'hypothèse d'une limitation alimentaire causée par les activités de filtration des dreissénidés comme cause du déclin, mais il est difficile d'établir des liens directs entre la perte des *Diporeia* et les indicateurs de disponibilité de nourriture.

[Traduit par la Rédaction]

Introduction

The increased spread of aquatic invasive species has led to the growing realization that these invaders, either individually or in concert, can change ecosystems at many levels of organization (Simon and Townsend 2003). A striking example is the Great Lakes ecosystem, where over the past 10–15 years, species invasions have led to the loss of native species, altered pathways of energy and nutrient flux through food webs, and redefined fundamental understanding of ecosystem function (Nalepa et al. 1996; Vanderploeg et al. 2002; Hecky et al. 2004). When considering imposed changes within the Great Lakes, perhaps the most large-scale, and certainly the most equivocal, has been the disap-

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pearance of the deepwater amphipod *Diporeia* spp. Declines in *Diporeia* populations have recently been documented in all the lakes except Lake Superior, and large areas in southeastern Lake Michigan (Nalepa et al. 1998), outer Saginaw Bay, Lake Huron (Nalepa et al. 2003), eastern Lake Erie (Dermott and Kerec 1997), and Lake Ontario (Dermott 2001; Lozano et al. 2001) are now mostly devoid of this organism.

Diporeia are part of a deepwater fauna that inhabit cold, proglaciated lakes, brackish estuaries, and coastal margins in the holarctic region (Bousfield 1989). Prior to its decline, *Diporeia* were the most abundant benthic macroinvertebrate in the deeper regions of all the Great Lakes, comprising >70% of all benthic biomass at depths greater than 30 m (Cook and Johnson 1974; Nalepa 1989). *Diporeia* were also present but less dominant in nearshore regions (<30 m) of the open main basins and naturally absent from the shallow, warm bays and basins (i.e., inner Green Bay, inner Saginaw Bay, western and central Lake Erie). As an infaunal detritivore, *Diporeia* burrow in the upper 2 cm of sediment and feed mainly on organic material freshly settled from the water column (i.e., mostly diatoms). Feeding rates reach a seasonal maximum during and just after the spring diatom bloom, and populations can consume a large portion of energy inputs to the benthic region during this period (Dermott and Corning 1988; Fitzgerald and Gardner 1993). *Diporeia*, in turn, are fed upon by most fish species found in the offshore waters of the Great Lakes, including slimy and deepwater sculpin (*Cottus cognatus* and *Myoxocephalus thompsonii*, respectively), alewife (*Alosa pseudoharengus*), bloater (*Coregonus hoyi*), lake whitefish (*Coregonus clupeaformis*), yellow perch (*Perca flavescens*), and rainbow smelt (*Osmerus mordax*) (Anderson and Smith 1971; Scott and Crossman 1973; Wells 1980). As such, it serves as an important pathway by which energy fixed as primary production is cycled to upper trophic levels.

Declines of *Diporeia* populations in the Great Lakes were first noted in the early 1990s, and in all lake areas, these declines were coincident with the introduction and spread of the invading species *Dreissena polymorpha* (zebra mussel) and *Dreissena bugensis* (quagga mussel). A common hypothesis for the decline is that dreissenids are outcompeting *Diporeia* for available food (Nalepa et al. 1998; Dermott 2001). Dreissenids filter-feed near the sediment surface, and this hypothesis assumes that settling organic material is intercepted by dreissenids before it reaches the upper sediments and becomes available to *Diporeia*. Deepwater amphipods such as *Diporeia* (neararctic) and the closely related *Monoporeia affinis* (palearctic) are generally food-limited, and both short- and long-term population trends have been attributed to changes in pelagic food inputs to the benthic region (Sarvala 1986; Johnson and Wiederholm 1992; Goedkoop and Johnson 2001). Yet despite the broad negative response of *Diporeia* to *Dreissena*, there are inconsistencies when examining decline patterns relative to the food-limitation hypothesis. For one, *Diporeia* populations have disappeared from several areas in the Great Lakes that were far-removed from dreissenid colonies and where potential food was still present in overlying waters and presumed to be settling to the bottom (Dermott 2001; Nalepa et al. 2003). Also, *Diporeia* are still abundant in some areas despite the presence of dreissenids (Dermott et al. 2005).

In this paper, we document recent spatial and temporal trends of *Diporeia* populations in Lake Michigan relative to expanding numbers of dreissenids. We also examine changes in age structure, physiological well-being, and pelagic food inputs during periods of population loss. These changes were compared with similar observations made prior to the introduction of dreissenids and *Diporeia* declines. Moreover, we conducted laboratory experiments to provide insights into our field observations and to further explore the food-limitation hypothesis.

Materials and methods

Spatial and temporal trends in densities

To document long-term spatial and temporal trends in densities of *Diporeia* and *Dreissena* in Lake Michigan, benthic samples were collected over several time periods at sites located in the southern basin and also at sites located throughout the entire lake. In the southern basin, samples were collected at 40 sites in 1998–2002 (Fig. 1). Bottom substrates at the sites ranged from coarse sand and gravel to fine silt, and depths ranged from 16 to 157 m. These 40 sites are part of a long-term monitoring program of the total macroinvertebrate community and have been sampled for 2 consecutive years every 5 years between 1980 and 1993 (Nalepa 1987; Nalepa et al. 1998). Consistent with this program, samples were again collected at these sites in 1998–1999. In 2000–2002, samples were collected at the same 40 sites and at 13 additional sites (A-4, C-2, C-45, F-2, F-3, G-45, K-2, N-2, N-3, T-3, M-45, R-45, SAU-45; Fig. 1). Whereas data from all 53 sites were used to better define spatial distributions of *Diporeia* and *Dreissena* in each of the 3 years, only data from the original 40 sites were used when examining temporal trends. Samples in 1998–1999 were collected in spring (mid-May to early June), summer (late July to early August), and fall (September to October), but in 2000–2002, samples were collected only in fall. For analysis purposes, sites were divided into four depth intervals: 16–30, 31–50, 51–90, and >90 m. These depth intervals are consistent with prior characterization of depth–macroinvertebrate associations in Lake Michigan (Nalepa 1987).

Densities of *Diporeia* and *Dreissena* were determined throughout Lake Michigan by sampling at 158 sites in late summer–fall 2000. Besides the 53 sites sampled in the southern basin, an additional 105 sites were sampled in the central and northern basins, Green Bay, and Grand Traverse Bay. Many of these sites (42 of 105) were sampled previously in 1994–1995 (Nalepa et al. 2000).

Methods of collection and analysis were the same for all sampling periods. Sediment samples were taken in triplicate with a Ponar grab (area = 0.046 m^2) at each site and washed into an elutriation device fitted with a nitex sleeve with 0.5 mm openings. Retained material was immediately preserved in 5% buffered formalin containing Rose Bengal stain. In the laboratory, all macrobenthic organisms in the 1998–1999 samples were picked, counted, and sorted into major taxonomic groups (Amphipoda, Oligochaeta, Chironomidae, *Dreissena*, Sphaeriidae) under a low-power magnifier lamp

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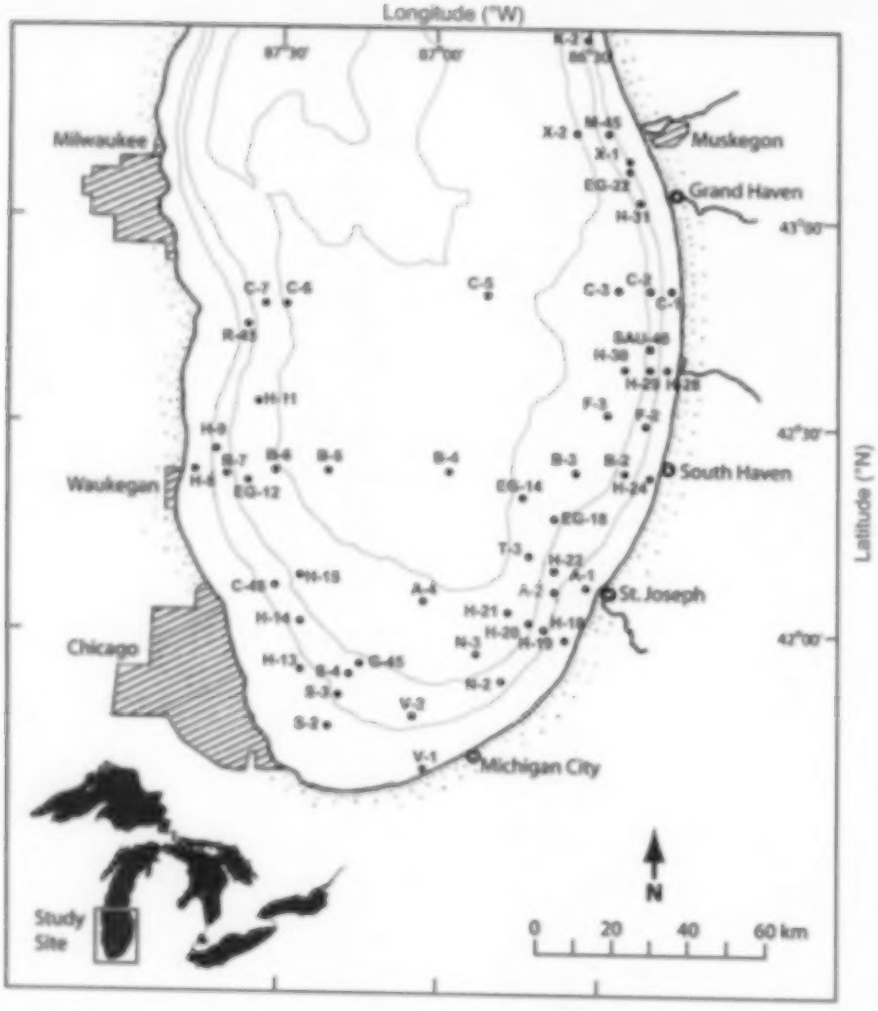
Fig. 1. Sampling sites in southern Lake Michigan, USA (inset shows location in the Great Lakes area). Depth contours are 25, 50, and 100 m.



(1.5σ). Chironomidae densities were low as in previous years and therefore not reported here. Only *Diporeia* and *Dreissena* were enumerated in samples collected in 2000–2002.

For the southern basin, differences in densities of *Diporeia* and *Dreissena* over the 1992–2002 period, as well as differences in densities of Oligochaeta and Sphaeriidae over the 1992–1999 period, were tested using a two-way analysis of variance (ANOVA; year × depth interval) on individual replicates. For the lakewide surveys in 1994–1995 and 2000, density differences of *Diporeia* and *Dreissena* were tested using a two-way ANOVA as above (period × depth interval). Additionally, the lake was divided into south, central, and north regions (Nalepa et al. 2000), and a two-way ANOVA (year × region) was used to test differences separately within each depth interval. For all ANOVAs in the southern basin and lakewide surveys, the data were log-transformed (ln + 1) to homogenize variances and post hoc multiple-range tests (Tukey's honestly significant difference (HSD)) were performed using Bonferroni-adjusted p values.

Population age structure, physiological condition, and physical variables

Soon after it became apparent that the *Diporeia* population in the southern basin was declining (Nalepa et al. 1998), we initiated a monthly sampling program in 1997 at four sites in the southeastern portion of the lake to document trends in age structure, lipid content, and length–weight and also to document relative amounts of potential food settling to the benthic region. The sites were located at 45 m water depth off St. Joseph (H-22; 42°08.35N, 86°39.83W), Saugatuck (SAU-45; 42°41.14N, 86°18.90W), Grand Haven (H-31; 43°02.47N, 86°19.99W), and Muskegon (M-45; 43°11.27N, 86°25.78W) (Fig. 1). Based on sampling prior to 1997, we knew that the state of populations at these four sites varied widely. The population had already disappeared at H-22, was present but declining at SAU-45 and H-31, and was still abundant at M-45. Both H-22 and H-31 were part of our long-term monitoring program, and SAU-45 was located near a long-term monitoring site of similar depth (B-2).

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Samples for density estimates of *Diporeia* and *Dreissena* at H-31 had also been collected one to four times per year in 1994, 1995, and 1996. In 1997 and 1998, Ponar samples at all four sites were collected monthly from late March–April to late October–November. After 1998, monthly sampling continued at sites where *Diporeia* were still present and lasted until it was no longer found.

Beginning in 1994 at H-31 and in 1997 at the other 45 m sites, body lengths of *Diporeia* in each of the replicate samples were determined by first tracing individuals (body midline) under 12× magnification using a camera lucida and then measuring tracings with a digitizer (Quigley and Lang 1989). Measurements were made from the base of the rostrum to the tip of the telson. In replicates with high numbers of individuals, animals were subsampled using a Folsom plankton splitter, and lengths were determined on at least 75–100 animals. In addition, body lengths were determined on animals in Ponar grabs collected monthly (April to November) at H-31 in 1986–1988. For these samples, all individuals in one replicate grab were measured. After lengths were determined, animals were placed into three size categories: 0–3, 3–5, and >5 mm. At depths of about 45 m in the Great Lakes, these sizes represent newly recruited young (YOY), juveniles, and adults, respectively (Winnell and White 1984; Johnson 1988).

On each sampling date beginning in 1994, extra Ponar grabs were taken at each site for the determination of *Diporeia* lipid content and length–weight. Upon collection, entire grab samples (animals, sediments, and overlying waters) were placed into plastic bags and kept cool during transport back to the laboratory. Within 24 h of collection, 20–25 juveniles and adults were placed individually into preweighed mini-test tubes (6 mm × 50 mm). For YOY, 5–10 individuals were placed into each tube (3–5 replicates). Before animals were placed into the tubes, individual body lengths were traced and later measured. The animals were dried for 48 h (under N_2 at 50–60 °C) and then stored frozen under vacuum until lipid extraction. Animals were reweighed just prior to lipid extraction, and individual animal weights were used to derive length – dry weight relationships. For YOY, mean length and weight were used in derived relationships. Total lipids were extracted using chloroform–methanol (2:1), quantified gravimetrically, and reported as percent dry weight (Gardner et al. 1985*a*). Differences in lipid content between years and age classes were examined with a two-way ANOVA after arcsine transformation.

Sediment traps were deployed at the 45 m sites to measure potential pelagic inputs to the benthic region. In 1997, settling material was collected with a sequencing sediment trap that consisted of a cylinder with a 20 cm opening and 8:1 aspect ratio (Muzzi and Eadie 2002). A bottom funnel led to an attached array of twenty-three 60 mL bottles within a rotating carousel. The carousal was programmed to rotate so a new bottle collected every 9 days. Before deployment, each bottle was filled with 30 mg mercuric chloride to prevent microbial activity. The traps were deployed just below the thermocline (30 m water depth) from March – early April to October 1997 at SAU-45, H-31, and M-45. In 1998 and 1999, sediment traps consisted of a cylinder with an opening of 10 cm and an aspect ratio of 5:1. The cylinder had a funnel at the bottom connected to a 500 mL bottle that had 20 mL chloroform as a preservative. Intercalibrations showed these traps collected at the same rate as the sequencing traps deployed in 1997 (Muzzi and Eadie 2002). Traps were deployed at all four 45 m sites in 1998 and at H-31 and M-45 in 1999. Traps were retrieved and bottles replaced on a monthly basis between March – early April and October.

After retrieval, collected material was poured through a 500 µm screen to remove benthos and large zooplankton and then allowed to settle for at least 24 h before the supernatant was decanted. The samples were then freeze-dried and kept frozen until analysis. Total organic carbon (TOC) was analyzed with a Carlos Erba CHN elemental analyzer. Prior to analysis, subsamples for TOC were treated with 2 mol·L^{-1} HCL, shaken for 24 h, and then dried at 60 °C to remove mineral carbonates. Chlorophyll *a* (Chl) was determined according to the method of Hansson (1988). Biogenic silica (BiS) was determined by first using a wet alkaline method for digestion and then measuring concentrations of SiO_2 with an Alpkem FS3000 analyzer (Krausse et al. 1983).

During each monthly sampling in 1998, an extra Ponar grab was collected at all four sites for determination of sediment TOC, BiS, and Chl. Monthly samples were also collected at H-31 in 1999 and at M-45 in 1999–2002. The top 0–1 cm of sediment was scraped from the surface of grab samples, freeze-dried, and analyzed as given above. Based on dated sediment cores collected in 2001, sediment accumulation rates at H-22 are about 1 cm·year^{-1} (J. Robbins, Great Lakes Environmental Research Laboratory, 2205 Commonwealth Boulevard, Ann Arbor, MI 48105, USA, unpublished data); thus, the 0–1 cm layer provided a good characterization of material deposited on an annual basis. Rates were likely less at the other 45 m sites, and this layer would therefore represent at least several years of accumulation. Grain size of sediment samples collected in 1998 was measured with a laser particle counter. Differences between years for individual constituents were tested with a one-way ANOVA, with sampling dates as within-year replicates.

Material collected in sediment traps consisted of material resuspended from the bottom by storm events and also of autochthonous material settled from the water column. To better define the latter source, a correction was made to calculated flux rates. Concentrations of TOC, BiS, and Chl measured for local surface sediment was subtracted from the concentration in the trapped material. This value was then multiplied by mass flux to produce an estimate of TOC, BiS, and Chl delivered to the site from sources other than local resuspension. Since not all sediment constituents were measured in 1997, corrections in that year were made based on 1998 values.

Laboratory experiments

Several laboratory experiments were conducted to provide insights into potential causes for the population decline. All experiments were conducted in a dark environmental chamber set at 4 °C. Purposes of the first experiment were to determine if sediments from a site where the population had recently disappeared were acutely toxic to *Diporeia* and to determine if these sediments had any nutritional value. Sediments were collected with a Ponar grab at two of the 45 m sites (H-31 and M-45) on 10 May 2000. At the time, mean densities of *Diporeia* were 0·m^{-2} and 6500·m^{-2} at the two

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sites, respectively. The top 1 cm of sediment from each site was scraped from grab samples, placed into prerinsed glass jars (500 mL), and kept cool. Experimental animals at M-45 were collected by placing entire grab samples into plastic bags and kept at 4 °C until the experiments were initiated.

Within 24 h of collection, sediments from each site were washed through a 0.5 mm screen to remove macroinvertebrates, allowed to settle, and then placed into glass scintillation vials (20 mL). Enough sediment was placed in the vials to achieve a depth of 2 cm, which is similar to *Diporeia*'s normal burrowing depth. Vials were filled with filtered lake water (0.45 µm Millipore filter) that had been collected from near bottom at M-45. There were four treatments: filtered lake water only, medium sand, H-31 sediment, and M-45 sediment. The sand was prerinsed and ashed at 550 °C for 1 h. All vials were placed into an aquarium filled with filtered, aerated lake water and allowed to stabilize for 24 h. After the stabilization period, one animal (>5 mm) was placed into each vial, and the vial was then covered with nitex screen (mesh opening 0.5 mm) to prevent animals from escaping and yet allowing water exchange to take place. As animals were placed into the treatment vials, 28 animals were randomly selected and frozen for later analysis of lipid content. On 21 May (10 days), 30 May (19 days), 21 June (41 days), and 16 July (66 days), at least 10 vials from each of the four treatments were removed and the animal's condition (live or dead) recorded. Lipid content of 5–10 living animals was measured as given above. Based on the volume of sediment in the vials (11.45 cm^2) and typical ingestion rates (Dermott and Corning 1988), experimental animals would have ingested only a small fraction (<1%) of the provided sediment during the 66-day experiment. The results were analyzed using a two-way ANOVA (treatment × day) after arcsine transformation. In the analysis, initial lipid content (day 0) for each treatment was derived by randomly assigning lipid content of the 28 pre-experimental animals to the treatments (n = 7 per treatment).

The second experiment consisted of preference–avoidance trials with sediments from H-31 and M-45. The purpose of this experiment was to determine if *Diporeia* actively avoided sediments from H-31, a site where populations had recently disappeared. On 14 July 2000, sediments (0–1 cm) from both sites were collected with a Ponar grab, placed into plastic bags, and kept cool. Within 24 h of collection, sediments were screened and placed into labeled Petri dishes (47 mm diameter × 1.5 cm depth), with six dishes per site. Three dishes from each site along with three dishes with ashed sand (control) were randomly placed into each compartment of a two-compartment aquarium containing filtered lake water. Thus, there were duplicate trials, with each trial having three replicates per treatment. After a 24 h stabilization period, 100 *Diporeia* (collected at M-45) were placed into each compartment. Dishes were carefully removed after 120 h, sediments washed through a 500 µm mesh screen, and the number of animals burrowed into each dish recorded. Differences among the three treatments were determined using a one-way ANOVA followed by Tukey's HSD. There were no significant differences between the two trials for each treatment (t test, df = 5, $P > 0.05$), so trial replicates were not distinguished in the ANOVA (n = 6 for each treatment).

Results

Density trends of major taxa groups in the southern basin, 1992–2002

Declines in *Diporeia* populations in the southern basin, which were initially documented in 1992–1993 (Nalepa et al. 1998), continued through 2002 (Table 1). Over the 1992–2002 period, significant differences in *Diporeia* densities occurred for years ($F_{[6,1751]}$ = 96.84, P = 0.0001), intervals ($F_{[3,1751]}$ = 249.50, P = 0.0001), and year × interval interaction ($F_{[18,1751]}$ = 11.95, P = 0.0001). Annual densities in 1998–2002 were not significantly different from each other but were significantly lower than densities found in 1992 and 1993 ($P < 0.05$, Tukey's HSD). Mean densities at the <30, 31–50, and 51–90 m intervals decreased by 89.4%, 90.5%, and 44.6%, respectively, between 1992 and 2002. Declines were more pronounced on the east side of the basin than on the west side as lower densities, first observed in the southeastern portion of the basin in 1992, extended farther north and offshore over time (Fig. 2). By 2002, *Diporeia* were rare or completely gone to depths of at least 50 m in an area from near Chicago to Grand Haven. Of 23 sites sampled in 2002 that were in less than 50 m water depth, *Diporeia* were present only at Stations H-8, B-7, and EG-12, all on the west side of the basin (densities 3155·m^{-2}, 4091·m^{-2}, and 3150·m^{-2}, respectively). Although still present, densities at these three sites in 2002 were lower than densities found in 1993 (declines of 46.2%, 46.2%, and 68.4%, respectively).

Whereas *Diporeia* continued to decline between 1992 and 2002, the dreissenid population became more widespread and abundant (Table 1). Differences in densities of *Dreissena* were significant for years ($F_{[6,1751]}$ = 13.43, P = 0.0001), intervals ($F_{[3,1751]}$ = 218.70, P = 0.0001), and year × interval interaction ($F_{[18,1751]}$ = 6.08, P = 0.0001). Over the 10-year period, dreissenids were mostly confined to depths <50 m, and greatest increases occurred at the 31–50 m interval. At this interval, mean densities of *D. polymorpha* increased from 7·m^{-2} in 1992 to 1112·m^{-2} in 2002. The other dreissenid species, *D. bugensis*, was first collected in the southern basin in 2001. By 2002, mean density at the 31–50 m interval had increased to 752·m^{-2} (Table 1). Mean density of the dreissenid population at the three west-side sites where *Diporeia* were still present in 2002 (H-8, B-7, and EG-12; total of nine replicates) were not significantly different from densities at the other 20 sites (total of 60 replicates) of similar depth (<50 m), where *Diporeia* had disappeared (t test, df = 67, P = 0.98, ln + 1 transformed).

Abundances of oligochaetes and sphaeriids in the southern basin were documented only in 1992–1993 and 1998–1999 (Table 1). Differences in oligochaete densities were significant for years ($F_{[3,1403]}$ = 2.99, P = 0.03), intervals ($F_{[3,1403]}$ = 84.88, P = 0.0001), and year × interval interaction ($F_{[9,1403]}$ = 5.34, P = 0.0001). Densities in 1993 were significantly lower than the other 3 years (P = 0.03, Tukey's HSD), but a consistent temporal trend over the entire 1992–1999 period was not apparent at any of the four intervals (Table 1). Sphaeriid densities were also significantly different for years ($F_{[3,1403]}$ = 12.29, P = 0.0001), intervals ($F_{[3,1403]}$ = 156.25, P = 0.0001), and year × interval interaction ($F_{[9,1403]}$ = 9.48, P = 0.0001). The general trend was

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Table 1. Mean (± standard error) densities (no.·m^{-2}) of the major taxa found in southern Lake Michigan in 1992–2002.

	Year						
Taxa	1992	1993	1998	1999	2000	2001	2002
16–30 m (n = 11)							
Diporeia	2618±504	2698±543	236±212	130±125	207±205	223±223	287±287
Oligochaeta	1713±376	1647±434	2367±600	2085±624	—	—	—
Sphaeriidae	1381±384	535±123	340±247	309±142	—	—	—
Dreissena polymorpha	389±253	1929±1698	978±255	2056±1014	617±340	193±74	885±464
Dreissena bugensis	0±0	0±0	0±0	0±0	0±0	3±3	117±63
31–50 m (n = 12)							
Diporeia	8710±759	7021±870	1957±883	892±450	1427±847	1364±798	665±395
Oligochaeta	4487±466	3166±330	4518±1146	6029±2219	—	—	—
Sphaeriidae	2273±303	1068±166	1434±294	707±162	—	—	—
Dreissena polymorpha	7±3	25±12	433±156	1059±414	865±555	1298±858	1112±755
Dreissena bugensis	0±0	0±0	0±0	0±0	0±0	5±5	752±495
51–90 m (n = 11)							
Diporeia	6380±332	5352±373	4593±1007	2380±577	3503±1185	2991±992	2963±959
Oligochaeta	2042±135	1530±97	2245±412	1986±345	—	—	—
Sphaeriidae	801±153	384±72	660±100	578±94	—	—	—
Dreissena polymorpha	1±1	1±1	5±3	3±2	8±5	13±7	20±15
Dreissena bugensis	0±0	0±0	0±0	0±0	0±0	0±0	8±5
>90 m (n = 6)							
Diporeia	3195±389	3226±515	4833±762	1794±249	2814±570	2608±392	3623±647
Oligochaeta	1179±151	1123±159	1009±176	1034±222	—	—	—
Sphaeriidae	113±30	98±36	197±99	154±84	—	—	—
Dreissena polymorpha	0±0	0±0	4±4	0±0	0±0	0±0	0±0
Dreissena bugensis	0±0	0±0	0±0	0±0	0±0	0±0	0±0

Note: Oligochaeta and Sphaeriidae were not sampled in 2000–2002. The number of sites (n) in each of the four depth intervals are shown in parentheses.

for a decline in densities at the two shallowest depth intervals over the period.

Lakewide density trends, 1994–1995 to 2000

Comparisons of lakewide densities in 1994–1995 and 2000 indicated that declines of *Diporeia* occurred not only in the southern basin but also throughout the lake (Fig. 3). Mean lakewide density was 65% lower in 2000 compared with 1994–1995, and this difference was significant ($F_{[1,234]}$ = 53.38, P = 0.0001). The decline occurred across all depth intervals, as the year × interval interaction was not significant ($F_{[3,234]}$ = 2.16, P = 0.09). Densities at the <30, 31–50, 51–90, and >90 m intervals were 77.9%, 73.7%, 53.2%, and 51.6% lower, respectively (Table 2). Further, the extent of the decline was greatest in the northern region; the overall decline was 91.4% in the north compared with 65.0% and 42.4% in the south and central regions, respectively. While densities were lower in the north in each of the four depth intervals, a regional difference was only significant at the >90 m interval ($F_{[2,34]}$ = 8.58, P = 0.001; Tukey's HSD, P < 0.003). Lakewide densities of *Dreissena* were significantly higher in 2000 compared with 1994–1995 ($F_{[1,236]}$ = 38.04, P = 0.0001). At sites <50 m, mean dreissenid densities were highest in the northern region in both sampling periods, which may explain greater declines of *Diporeia* in this portion of the lake.

Annual density trends, 45 m sites

From the long-term monitoring program, densities of *Diporeia* were available for three of the 45 m sites (H-22, SAU-45, and H-31) in 1980–1981 and 1986–1987, which were the years just prior to the first report of *Dreissena* in Lake Michigan (first reported in 1989; Marsden et al. (1993)). Mean annual density of *Diporeia* by site and year ranged from 5347 to 14 044·m^{-2} (Fig. 4). Beginning in 1992, the population declined systematically, first at the southern-most site (H-22) and later at the more northern sites. By fall 2002, *Diporeia* had disappeared from all four sites (Figs. 4, 5). Whereas *Diporeia* disappeared from each site within a 10-year period, rates and patterns of decline were site-specific. In 1992, densities at H-22 declined from 10 600·m^{-2} in spring to 200·m^{-2} in fall, a 98% decline in just 6 months. Declines to total loss were more gradual at the other 45 m sites, occurring between 1994 and 1999 at H-31 and between 1997 and 2002 at M-45. Unlike populations at the other 45 m sites, the population at M-45 recovered somewhat after initial declines were observed. Densities increased throughout 1999 and remained higher into spring 2000; however, densities decreased thereafter (Fig. 5). When considering all four 45 m sites, the period of time in which *Diporeia* declined from densities of 5300–14 000·m^{-2} to <200·m^{-2} varied from 0.5 to 5 years.

The relationship between annual densities of *Diporeia* and *Dreissena* was examined over the time period between just

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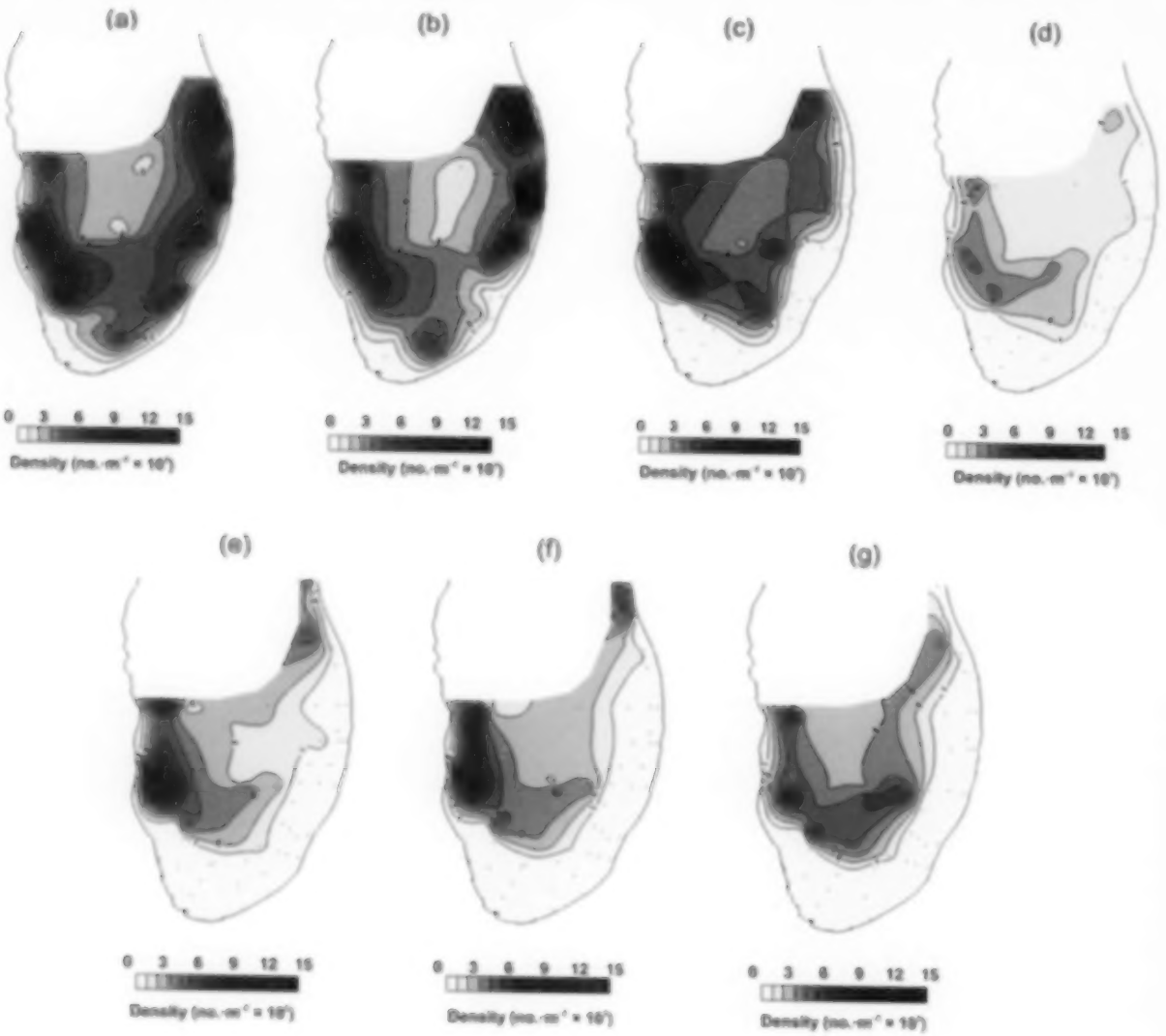
Fig. 2. Mean density (no.·m^{-2} × 10^3) of *Dreissena* spp. in southern Lake Michigan. Small crosses denote sampling sites. (*a*) 1992, (*b*) 1993, (*c*) 1998, (*d*) 1999, (*e*) 2000, (*f*) 2001, (*g*) 2002.



prior to initial declines and total disappearance. Densities of *Dreissena* and *Dreissena* were not well correlated at H-22; the population at this site collapsed in 1992 and totally disappeared by 1997, but *Dreissena* was not found at this site until 2000 (Table 3). At H-31 the relationship between the two taxa over the 1992–1999 period was not significant (linear regression; $R^2 = 0.37$, $P = 0.11$), but the residuals indicated the presence of autocorrelation (Durbin-Watson D statistic = 0.966). Further analysis with a 1-year time lag ($t - 1$) in *Dreissena* densities provided a significant relationship ($R^2 = 0.70$, $P = 0.02$, Durbin-Watson D statistic = 1.97). The relationship was improved when data from M-45 was included (Fig. 6).

Recruitment and age classes, 45 m sites

Because of limited availability of seasonal, size frequency data collected prior to declines at H-22 and SAU-45, meaningful analysis of density trends in the various age classes was only possible for populations at H-31 and M-45. As noted, declines in population density at H-31 were initially observed in 1994. Based on relative densities of YOY, juveniles, and adults, lower density in this year was a result of poor recruitment. Mean annual density of YOY in 1994 was only 215·m^{-2} (seasonal peak = 406·m^{-2}) compared with a range of 920–2438·m^{-2} (seasonal peak = 2411–4895·m^{-2}) in 1986–1993. In contrast, mean densities of juveniles and adults in 1994 were within the range found in 1986 to 1993 —

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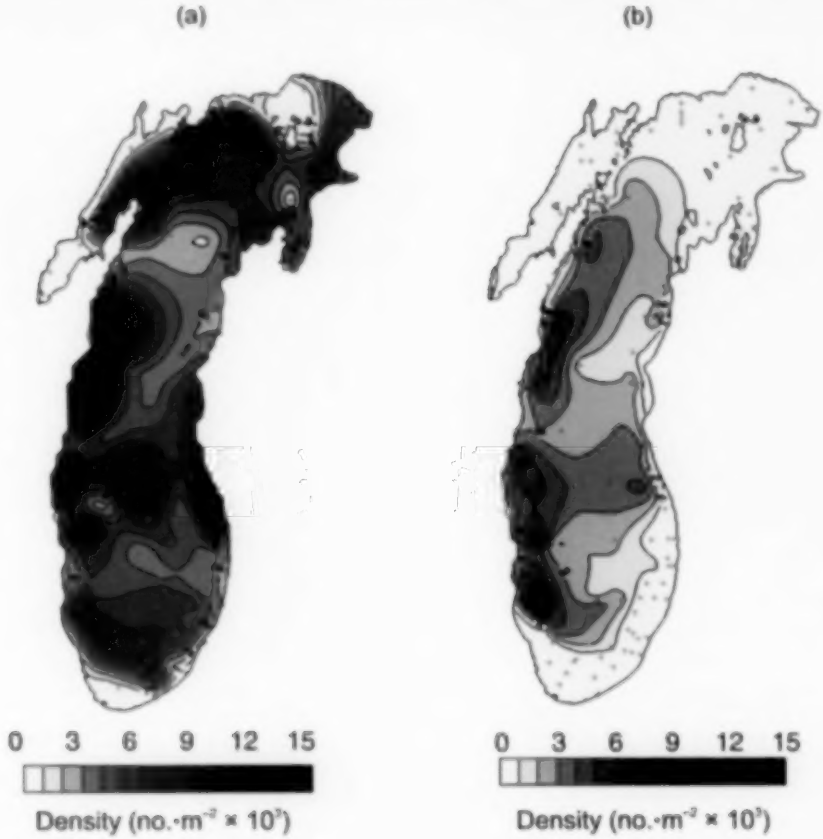
Fig. 3. Mean density (no.·m^{-2} × 10^3) of *Diporeia* spp. throughout Lake Michigan. Small crosses denote sampling sites. (*a*) 1994–1995, (*b*) 2000.



juvenile density was 3860·m^{-2} in 1994 compared with 2004–4283·m^{-2} in 1986–1993, and adult density was 3588·m^{-2} in 1994 compared with 3462–7173·m^{-2} in 1986–1993. Considering *Diporeia* have a 2-year life cycle at this depth in southeastern Lake Michigan (Winnell and White 1984), the lack of recruitment in 1994 likely accounted for lower juvenile densities observed in 1995 (Fig. 7). Recruitment in 1995–1997 was generally similar to recruitment in 1986–1993, as strong peaks in YOY occurred in 1995 (2438·m^{-2}) and 1997 (2640·m^{-2}), and although we only sampled on one date in 1996 (July), a relatively high density of YOY (2202·m^{-2}) indicated recruitment also occurred in that year. Despite good recruitment, juvenile densities in these 3 years remained lower than found in 1986–1994, indicating poor YOY survival. Juvenile densities at H-31 subsequently collapsed in 1997, declining from 3300·m^{-2} in early spring to 150·m^{-2} in late fall. Adult densities remained stable in 1997 but declined in 1998, most likely a result of the lack of juveniles the previous year.

At M-45, annual recruitment occurred between 1997 and 2002, and peaks in YOY densities ranged from 1200·m^{-2} to 4700·m^{-2} (Fig. 8). Yet despite recruitment, juvenile densities generally declined each year, again indicating poor YOY survival. The exception to this pattern occurred in 1999. YOY survival was high in 1999 as evidenced by an increase in juvenile densities throughout the year, peaking at 3500·m^{-2} in November; this accounted for the increase in population density in that year (Fig. 5). Juveniles continued to grow and survive through winter 2000 as evidenced by high adult density in spring 2000 (4000·m^{-2}). Recruitment occurred in 2000, but as in 1997 and 1998, these recruits did not survive to become juveniles.

The number of eggs per gravid female was determined in spring 2001 at M-45 to determine if brood size had declined since the 1980s. In a 1981 study at a 42 m site in southeastern Lake Michigan, Winnell and White (1984) found that brood size ranged from 10 to 25 eggs per female and was directly related to female size. Brood size in 2001 varied from 21 to 32 eggs per gravid female (n = 7) and fit the same functional relationship to female size as in 1981.

Lipid content and length–weight, 45 m sites

When densities at the 45 m sites were declining, lipid content of juvenile and adult *Diporeia* tended to increase (Fig. 9). Detailed analysis of trends between density and lipid content were restricted to M-45, since densities at the other 45 m sites were already declining prior to 1997. Between 1997 and 2001, there was a significant difference

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Table 2. Mean (± standard error) densities (no. m^{-2}) of *Diporeia* and *Dreissena* at four depth intervals in Lake Michigan in three different regions in 1994–1995 and 2000.

	Diporeia		*Dreissena*	
Lake region	1994–1995	2000	1994–1995	2000
<30 m				
South (7,11)	3488±1842	207±205	414±132	617±340
Central (2,16)	2173±2852	1794±655	0±0	2541±848
North (9,20)	2897±1156	77±34	926±921	2025±594
Overall	3124±916	692±252	623±457	1871±399
31–50 m				
South (6,20)	6306±1454	1194±561	48±42	589±338
Central (2,11)	10 477±4088	4702±1210	89±82	629±217
North (5,16)	4462±2150	100±39	528±528	2268±1353
Overall	6249±1243	1642±444	239±201	1170±489
51–90 m				
South (20,15)	5285±423	2742±932	<1±<1	6±4
Central (5,19)	11 997±1189	4691±487	0±0	32±16
North (6,12)	6262±925	893±414	0±0	7±5
Overall	6550±570	3064±437	<1±<1	17±7
>90 m				
South (9,6)	4466±335	2814±570	0±0	0±0
Central (9,6)	4443±627	2818±836	0±0	0±0
North (5,5)	5007±1567	754±459	0±0	0±0
Overall	4567±414	2209±429	0±0	0±0

Note: See Nalepa et al. (2000) for delineation of regions. Values in parenthesis are numbers of sites sampled in 1994–1995 and 2000, respectively, within each depth interval and lake region. In 1994–1995, all *Dreissena* were *D. polymorpha*; in 2000, 98.3% were *D. polymorpha* and 1.7% were *D. bugensis*.

between years ($F_{(3,681)}$ = 62.41, P = 0.0001), age classes ($F_{(2,681)}$ = 10.62, P = 0.0001), and year × age class interaction ($F_{(13,681)}$ = 10.60, P = 0.0001). Yearly means in 1999–2001 were significantly higher than those in 1997–1998 (P = 0.0001, Tukey's HSD), and lipid content in juveniles and adults were significantly higher than those in YOY (P = 0.0001 Tukey's HSD). When just considering juveniles and adults, lipid levels increased from 21.6% ± 0.42% in 1997–1998 to 28.7% ± 0.56% in 1999–2001. Similarly, as densities declined at H-31 between 1997 and 1999, mean adult lipid content increased from 23.9% ± 0.6% in 1997 to 34.7% ± 2.1% in 1999. The relationship between lipid content and density can be put into a more long-term perspective by examining trends at H-31 beginning in the 1980s (Fig. 4). Seasonal trends in lipid content of adult *Diporeia* were measured at this site in 1984, 1986, 1988, and 1989 (Gardner et al. 1985*b*; Gauvin et al. 1989; Cavaletto et al. 1996). Mean annual lipid content in 1984–1989 varied from 26% to 32%. When density declines were first observed in 1994, mean lipid content was only 15%. As densities continued to decline after 1994, lipid content increased each successive year until by 1998–1999 lipid values were as high as found in the 1980s.

Lipid content in juveniles and adults generally peaked in spring or summer and then declined in fall (Fig. 9). Seasonal peaks in late spring – summer were consistent with the premise that intensive feeding during the spring diatom bloom results in the storage of energy as lipids (Gardner et al. 1985*b*, 1990). To determine if seasonal peaks in 1997–2001 were comparable with those found in 1984–1989 (adults only), the seasonal maximum was divided by the early spring minimum and the ratio was compared between the two periods. For the 1997–2001 period, only those sites and years in which adults were collected throughout the year were included. The mean ratio was 1.31 ± 0.07 (n = 8) in 1997–2001 and 1.58 ± 0.28 (n = 4) in 1984–1989. Although lower in the 1997–2001 period, the difference was not significant (t test; $P > 0.05$).

In deepwater amphipods, weight per unit length generally declines when animals are food-limited (Hill et al. 1992; Lehtonen 1996). The relationship between lipid-free dry weight (LFDW in mg) and length (L in mm) was defined by LFDW = aL^b and was determined annually for each 45 m site over the 1994–2001 period (Table 4). All regressions were significant (range of R^2: 0.56–0.96). When LFDW for a standard 5 mm animal was calculated, yearly trends were not apparent (Table 4).

Sedimentation rates and sediment variables

Sediment traps, deployed at the 45 m sites in 1997–1999, documented amounts of organic material settling to the bottom that potentially served as a food source for *Diporeia*. In general, there was a consistent primary peak of TOC, BiS, and Chl in spring and a secondary peak in fall at each of the sites (Fig. 10). Most relevant to *Diporeia* populations were flux rates associated with the spring peaks; these peaks are enriched in organic materials (diatoms) compared with peaks in the fall (Scavia and Fahnenstiel 1987; Gardner et al.

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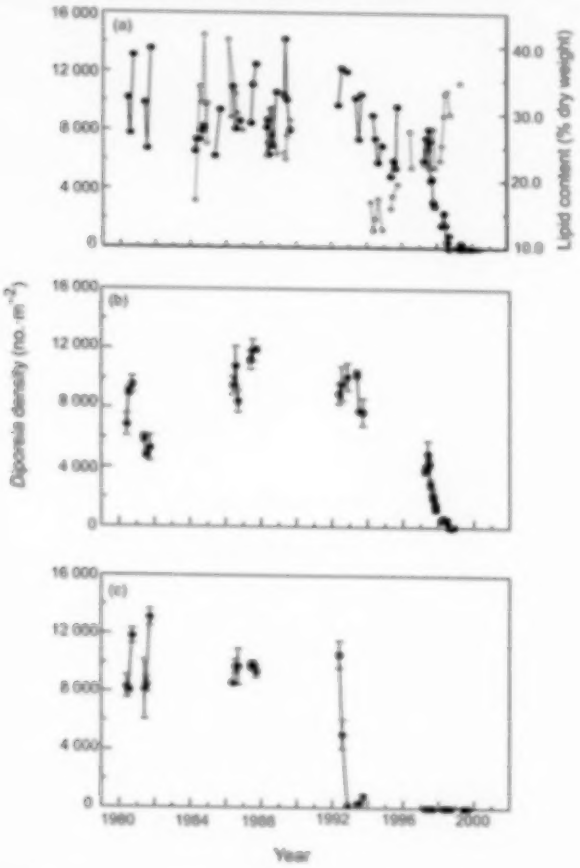
Fig. 4. Density (no.·m^{-2}) of *Diporeia* spp. at three 45 m sites in southeastern Lake Michigan, 1980–2002: (*a*) H-31, (*b*) SAU-45, (*c*) H-22. The broken lines at H-31 give the lipid content (percent dry weight) of *Diporeia* spp. at this site.



1989). Over the 1997–1999 period, the magnitude of spring peaks at H-31 and M-45 decreased for all constituents (Fig. 10). In spring 1997, the spring average (March–May) flux rates of TOC at these two sites were 434 and 461 mg·m^{-2}·day^{-1}, respectively, and flux rates of BiS were 1176 and 1199 mg·m^{-2}·day^{-1}, respectively. In contrast, spring 1999 flux rates of TOC were only 88 and 57 mg·m^{-2}·day^{-1}, and flux rates of BiS were 181 and 45 mg·m^{-2}·day^{-1}, respectively, for sites H-31 and M-45. Low flux rates in 1999 were mostly related to quantitative changes in inputs, as nutrient content of collected material was generally higher in 1999 than in previous years (Table 5). Further, mean annual C/N ratio (weight) did not show a consistent trend at these two sites over the same period; the ratio tended to increase at M-45 but not at H-31. In 1998 when flux rates were measured at all four 45 m sites, spring average flux rates of all constituents increased on a spatial gradient from south to north, being lowest at H-22 and highest at M-45 (Fig. 10), while the mean C/N ratio decreased along the same gradient (Table 5).

Sediment composition varied widely at the 45 m sites, ranging from predominately silt at the southern-most site (H-22) to sand at the northern-most site (M-45). The percent

Table 3. Mean (± standard error) density (no.·m^{-2}) of *Dreissena* at the 45 m sites in southeast Lake Michigan, 1992–2002.

	Station			
Year	H-22	SAU-45	H-31	M-45
1992	0±0	0±0	3±2	—
1993	0±0	0±0	14±9	—
1994	—	—	39±14	—
1995	—	—	50±16	—
1996	—	—	143	—
1997	0±0	30±17	669±261	616±367
1998	0±0	966±897	2561±853	1044±525
1999	0±0	21	2581±209	2235±1075
2000	21	136	171	836±459
2001	0	0	3576	1046±646
2002	29	464	1699	835±376

Note: Standard errors depict variability between sampling dates.

Fig. 5. Mean density (no.·m^{-2}) of *Diporeia* spp. on each sampling date at three 45 m sites in 1997–2002. Although not shown, no *Diporeia* were collected at the other 45 m site (H-22) during the sampling period. Error bars denote standard error. △, SAU-45; ○, H-31; ●, M-45.

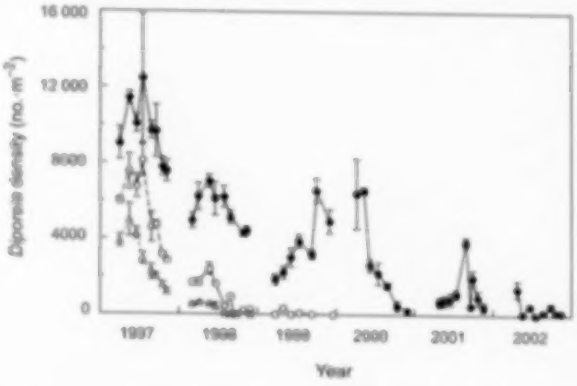


Fig. 6. Relationship between mean annual density (no.·m^{-2}) of *Diporeia* spp. and *Dreissena* at H-31 (●) and M-45 (○). *Dreissena* densities are given as a 1-year time lag (t – 1). Sampling periods were 1992–1999 for H-31 and 1997–2002 for M-45 (linear regression R^2 = 0.59, P = 0.003, n = 12).

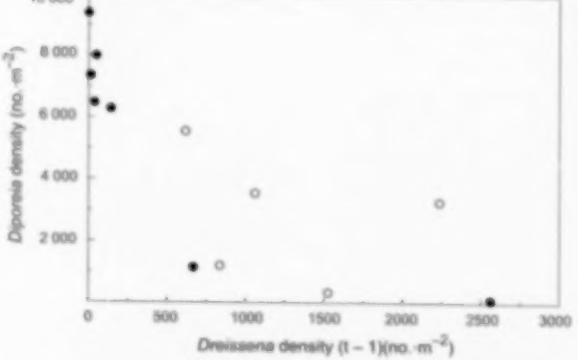


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Fig. 7. Density (no.·m^{-2}) of three life stages of *Diporeia* spp. at H-31 in 1986–1999: (*a*) young-of-year, (*b*) juveniles, (*c*) adults.

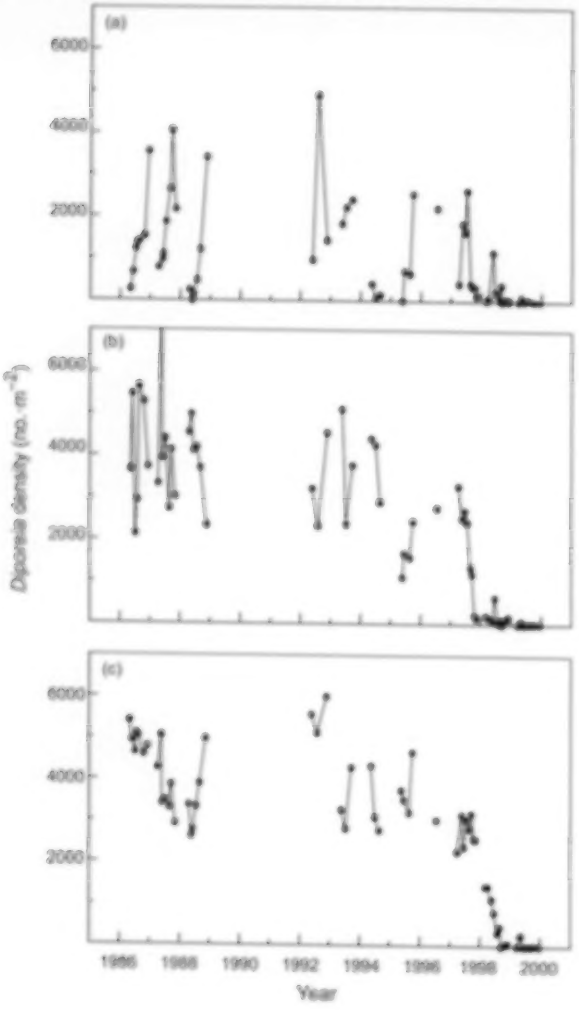
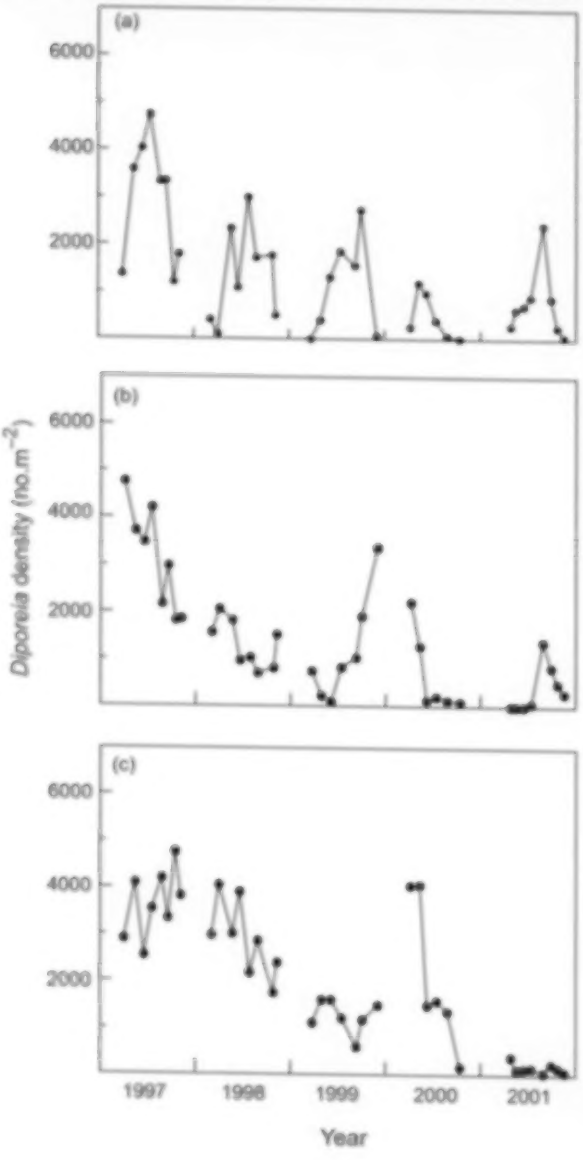


Fig. 8. Density (no.·m^{-2}) of three life stages of *Diporeia* spp. at M-45 in 1997–2001: (*a*) young-of-year, (*b*) juveniles, (*c*) adults.



clay, silt, and sand was, respectively, 2.3%, 85.7%, and 12.0% at H-22; 1.9%, 53.2%, and 44.9% at SAU-45; 1.7%, 31.3%, and 67.0% at H-31; and 0.7%, 15.2%, and 84.1% at M-45. Nutrient content of the upper 0–1 cm decreased from south to north as grain size increased. In 1998 mean sediment concentrations of TOC, BiS, and Chl were 4-, 6-, and 3.5-times greater, respectively, at H-22 than at M-45 (Table 5). Continued sampling at H-31 to 2000 and at M-45 to 2002 indicated nutrient content increased over levels found in 1998. At H-31 there was a significant difference between years (1998–2000) for BiS ($F_{[2,11]} = 4.406$, $P = 0.039$), and at M-45 there was a significant difference between years (1998–2002) for TOC ($F_{[4,20]} = 12.43$, $P = 0.0001$), BiS ($F_{[4,20]} = 18.77$, $P = 0.0001$), and Chl ($F_{[4,20]} = 11.122$, $P = 0.0001$). The increase at M-45 was such that in 2002, concentrations of BiS and Chl were not significantly different from values found at H-22 in 1998 (t test, df = 15, $P = 0.239$ for BiS; $P = 0.79$ for Chl). As nutrient content increased, there was no apparent trend in the C/N ratio (Table 5).

Laboratory experiments

Mortality in the 66-day starvation experiments was low in all four treatments. Of the 191 animals retrieved from filtered lake water, ashed sand, H-31 sediments, and M-45 sediments, only five were found dead during the entire experimental period. Lipid content declined in all four treatments during the experimental period (Table 6). Mean initial lipid content was 31.8% on day 0, and final lipid content ranged from 21.3% (H-31 sediment) to 25.2% (sand) on day

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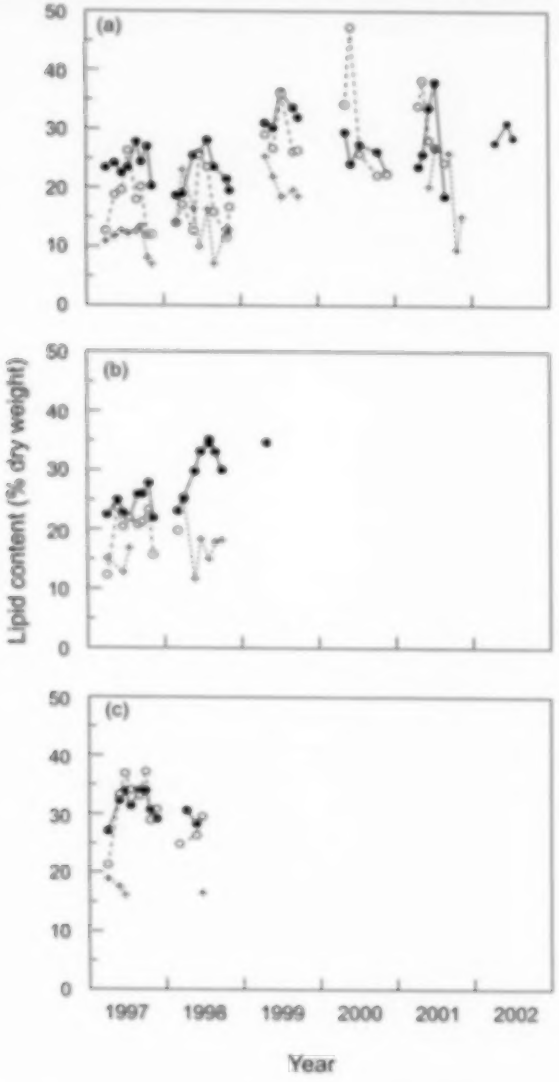

Fig. 9. Mean lipid content (percent dry weight) of young-of-year (+ - - +), juvenile (○ - - ○), and adult (● — ●) *Diporeia* spp. at three 45 m sites in 1997–2001: (*a*) M-45, (*b*) H-31, (*c*) SAU-45.

66. There was a significant difference between dates ($F_{[4,109]} = 6.46$, $P = 0.0001$), but date × treatment interaction was not significant ($F_{[12,109]} = 0.95$, $P = 0.50$), indicating no difference in treatment effects. On the date experiments ended (16 July), mean lipid content of freshly collected adults at M-45 was 27.4%. The greater lipid value of in situ animals suggested access to nutritional material not available to laboratory animals.

In the preference–avoidance experiments, 95 of 100 and 92 of 100 animals were recovered in the two trials, respectively. Mortality was minimal (only 6 of 187), and all living animals were found burrowed in the substrate rather than swimming in the overlying waters. Mean (± standard error, SE) numbers of animals burrowed in sand, H-31 sediment, and M-45 sediment were 0 ± 0, 14.5 ± 2.5, and 15.7 ± 3.5, respectively. Numbers found in the two sediment treatments were not significantly different, and numbers in both sediment treatments were significantly higher than numbers found in the sand treatment ($F_{[2,15]} = 12.268$, $P = 0.001$, Tukey's HSD). When sediments for these experiments were collected (July 2000), the *Diporeia* population had already disappeared from H-31, but was still present at M-45. Given these laboratory results, the disappearance from H-31 was not likely due to animals actively avoiding the sediments per se.

Discussion

On a broad scale, the decline of *Diporeia* in Lake Michigan in the 1990s was closely related to the expansion of dreissenid populations within the lake. In the southern basin, greatest declines occurred in the 30–50 m depth interval where dressenid densities increased to the greatest extent. Also, declines lakewide were most extensive in the northern portion of the lake where dreissenid densities were higher than in more southern portions. Yet on a local scale, inconsistencies were apparent. Whereas *Diporeia* and dreissenids were negatively correlated at several sites, *Diporeia* remained abundant at some sites despite the long-term presence of dreissenids, but yet declined rapidly at a site with no dreissenids. Our field observations and laboratory experiments failed to establish a clear, direct relationship between the loss of *Diporeia* and indicators of food availability. From our results, several questions pertinent to the food-limitation hypothesis remain enigmatic. (*i*) Why did the *Diporeia* population collapse so completely in an area where there were no mussels and where at least some pelagic food material was still likely settling to the benthic region? (*ii*) Why did lipid content, which is an indicator of energy reserves and directly related to food availability, remain at high levels as the population disappeared?

In areas where dreissenids were not present or found in low numbers, such as at H-22, sediment traps should accurately reflect pelagic inputs to the upper sediments. That is, mussels at the sediment surface would not be intercepting settling organic material prior to becoming available to *Diporeia* feeding in the upper sediments. *Diporeia* at H-22 completely disappeared by 1997, yet based on trap flux rates of TOC, BiS, and Chl in 1998, at least some organic material was still settling to the bottom. Others have also documented a collapse of *Diporeia* populations in areas far removed from *Dreissena* colonies and where potential food was still found in the water column (Dermott 2001; Nalepa et al. 2003). Dermott (2001) theorized that the remote loss of *Diporeia* might be a function of their spatial distributions relative to dreissenid beds and dominant current patterns. Particulate organic material in water flowing over dreissenid beds would be removed by mussel filtration and unavailable to *Diporeia* located in areas downcurrent. In the Hudson River, Strayer and Smith (2001) suggested that the upstream removal of organic material by dense dreissenid colonies led to the severe decline of microzooplankton in areas downstream with few mussels. This, in turn, led to the extirpation of downstream *Chaoborus* populations, which relied on microzooplankton as a food source. Even so, it is difficult to reconcile how the remote removal of potential food by

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Table 4. Relationship between lipid-free dry weight and length for *Diporeia* at each of the 45 m sampling sites in each year lipid content was measured.

Year	*a*	*b*	*n*	R^2	5 mm
SAU-45					
1997	−4.497 (0.092)	2.484 (0.053)	195	0.919	0.61
1998	−4.880 (0.155)	2.660 (0.081)	73	0.939	0.55
H-31					
1994	−2.374 (0.194)	1.227 (0.114)	94	0.558	0.67
1995	−4.332 (0.208)	2.138 (0.113)	60	0.861	0.41
1996	−3.946 (0.338)	1.910 (0.169)	43	0.756	0.42
1997	−4.900 (0.081)	2.705 (0.048)	208	0.939	0.58
1998	−4.499 (0.147)	2.472 (0.081)	149	0.865	0.59
M-45					
1997	−4.838 (0.072)	2.666 (0.043)	172	0.957	0.58
1998	−5.086 (0.064)	2.732 (0.038)	205	0.962	0.50
1999	−4.803 (0.106)	2.679 (0.063)	107	0.946	0.61
2000	−5.222 (0.309)	2.833 (0.181)	97	0.721	0.52
2001	−4.975 (0.095)	2.678 (0.058)	116	0.950	0.51

Note: The relationship is defined by $\ln \text{LFDW} = a + b \ln L$, where LFDW is lipid-free dry weight (mg), and L is body length (mm). Standard error is given in parentheses. n is the total number of animals analyzed. The lipid-free dry weight of a standard 5 mm animal is given.

dreissenids in shallow, nearshore regions can so effectively eliminate *Diporeia* populations from deeper depths in southeastern Lake Michigan. In this area of the lake, nearshore–offshore transport of particulate material occurs mainly during storm events in the spring (Eadie et al. 2002). Dreissenid colonies can conceivably affect this transport process by retaining more organic matter in the nearshore zone, thus reducing deposition in offshore areas (Hecky et al. 2004). The role of nearshore transport compared with local pelagic inputs in supporting offshore *Diporeia* populations is unknown. Yet if nearshore retention of organic material by dreissenids was the reason for the total loss of *Diporeia*, then the population at 45 m must have been far more nutritionally dependent on inputs from the nearshore than pelagic inputs from the immediate overlying waters. This seems unlikely, since ingestion rates, assimilation rates, and lipid levels were closely linked to water column productivity at 45 m in the years prior to *Dreissena* (Fitzgerald and Gardner 1993; Gardner et al. 1989). In terms of food quality, C/N ratios of trap material and upper sediments at H-22 were 10–13, similar to the ratio of autochthonous matter produced by decomposed plankton (Wetzel 2001). Fresh algal material has a ratio of 6.7 (Redfield ratio). Ratios at H-22 were generally higher than ratios at the other 45 m sites, but below the threshold known to affect growth and development of some benthic detritivores (Soderstrom 1988; Dorgelo and Leonards 2001). While densities of deepwater amphipods are a function of fresh algal inputs (Johnson and Wiederholm 1992), the relationship between food quality and the survival of the population remains unclear. However, *Diporeia* have historically been the dominant benthic macroinvertebrate in the deepest regions of the Great Lakes where benthic food inputs are minimal and highly refractive. Further, the rapid decline at H-22 was first observed after the spring period, which is inconsistent with the food-limitation hypothesis, since this is the period when food availability would be at a seasonal maximum.

The disappearance of *Diporeia* at H-31 and M-45 was more gradual (5 years) than at H-22 and well correlated to an increase in the *Dreissena* population. Given this close temporal association, food limitation may indeed have played a major role in the loss of *Diporeia* at these sites. Yet flux rates of constituents indicative of food inputs during the period of initial declines were similar to rates reported prior to *Dreissena*. For instance, the population at H-31 began to decline in 1994 and collapsed in 1997 and 1998, while the population at M-45 began to decline in 1997. In 1997 and 1998, average spring flux rates of TOC at these two sites varied from 273 to 461 $mg \cdot m^{-2} \cdot day^{-1}$, which were comparable with rates of 288 and 430 $mg \cdot m^{-2} \cdot day^{-1}$ found at H-31 in 1986 and 1990, respectively (B.J. Eadie, unpublished data). Uncorrected mean spring flux rates of BiS in 1997–1998 were 433–1500 $mg \cdot m^{-2} \cdot day^{-1}$. These rates were generally similar to or greater than an uncorrected mean spring flux rate of 475 $mg \cdot m^{-2} \cdot day^{-1}$ found at H-31 in 1986 (Gardner et al. 1989). Populations were already declining in 1999 when far lower flux rates of all constituents were observed. Low flux rates in 1999 were likely a result of an uncommon occurrence rather than the beginning of a trend. In most years, water column Chl peaks in spring, but in 1999, the peak occurred in early winter (B.J. Eadie, unpublished data). Thus, we likely missed the spring diatom peak with our deployment in 1999. As noted, sediment traps do not reflect pelagic inputs to the upper sediments in areas when *Dreissena* densities are high. *Dreissena* densities were $>500 \cdot m^{-2}$ in 1997 at H-31 when the *Diporeia* population collapsed, but $<50 \cdot m^{-2}$ in 1994 when initial declines were observed. Thus, despite high pelagic inputs that were still likely present in 1994, even low densities of *Dreissena* had a negative impact on *Diporeia*.

Our laboratory experiments indicated that sediments from H-31 and M-45 did not have an adverse impact on *Diporeia* per se. Mortality was not observed after a 66-day exposure, and the sediments were not actively avoided. Interestingly,

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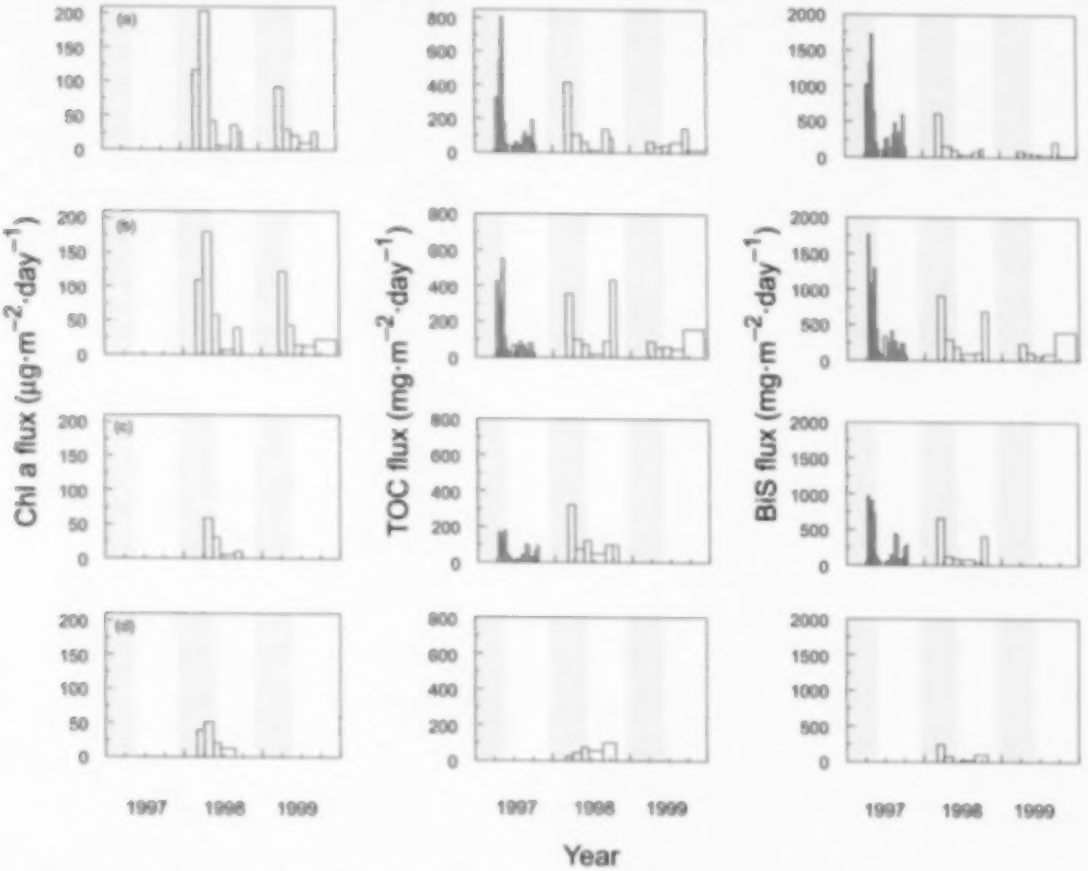
Fig. 10. Flux rates for chlorophyll *a* (Chl *a*), total organic carbon (TOC), and biogenic silica (BiS) at the 45 m sites in 1997–1999: (*a*) M-45, (*b*) H-31, (*c*) SAU-45, (*d*) H-22. Rates were derived from material collected in sediment traps placed at 30 depth in the water column. The input from local resuspension was corrected for by subtracting local surface sediment concentrations from trap concentrations, then multiplying by the mass flux. Shaded areas indicate unstratified periods.



whereas there was no mortality during the laboratory experiments, the population of *Dreissena* at M-45 declined by 66% over the same 66-day period (May to July). Thus, conditions that led to the decline at M-45 were not duplicated in the laboratory using sediments from the same site and animals from the same population. This may imply that the population was reacting negatively en masse to the physical deposition of organic material in the spring. As noted, the rapid decline at H-22 was similarly observed after the spring period. Sediments from H-31 and M-45 were not acutely toxic to *Diporeia*, the same result found for sediments from H-22 (Landrum et al. 2000).

If food limitation was the primary cause for the loss of *Diporeia*, then the animals should show some physiological signs of starvation before or during the period of population loss. In deepwater amphipods, lipid levels are a good indicator of food availability; levels increase just after the spring diatom bloom when food is readily available and decline during periods of low benthic food inputs in late summer and winter (Gardner et al. 1985*b*; Hill et al. 1992; Lehtonen 1996). When the population began to decline at H-31 in 1994, mean annual lipid content was only 15%, and the spring lipid peak was only 17%. These values indicate severe starvation — similar levels were found in laboratory animals starved for 120 days (Gauvin et al. 1989). Recruitment was poor in 1994, which is consistent with the suggestion that lipid values below 20% lead to reproductive failure (Hill et al. 1992). As densities continued to decline after 1994, lipid content unexpectedly increased and annual recruitment occurred. Possibly, lipid content increased because declining densities led to more food for remaining organisms. Yet if this were so, then poor YOY survival should not have occurred, and the population should have stabilized at some reduced level consistent with a diminished food supply. Further, the increase in dreissenids over this period would have further reduced available food and resulted in lower rather than higher lipid values. As *Diporeia* densities approached zero in 1999, lipid levels were over 30% and comparable with levels found at this site in the 1980s just after the spring diatom bloom (Gardner et al. 1985*b*; Cavaletto et al. 1996).

While the long-term decrease and then increase in lipid content found at H-31 has not been previously documented in field populations, such a pattern was found in animals

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Table 5. Mean (± standard error) annual concentrations of total organic carbon (TOC), biogenic silica (BiS), chlorophyll (Chl), and C/N ratio (weight) in material collected in sedimentation traps and upper sediments (0–1 cm) at the 45 m sites.

	TOC ($mg \cdot g^{-1}$)		BiS ($mg \cdot g^{-1}$)		Chl ($\mu g \cdot g^{-1}$)		C/N ratio	
Year	Trap	Sediment	Trap	Sediment	Trap	Sediment	Trap	Sediment
M-45								
1997	41.7±3.0	3.3±0.2	120.5±11.8	—	—	—	8.1±0.1	7.5±0.1
1998	47.8±8.7	4.7±0.3	70.5±23.5	2.6±0.3	24.7±5.9	1.1±0.2	9.3±0.7	7.7±0.4
1999	80.2±22.3	4.9±0.4	74.3±9.8	3.1±0.5	42.4±5.5	1.7±0.2	13.7±2.7	8.8±0.7
2000	—	5.0±0.3	—	2.1±0.6	—	0.8±0.2	—	8.5±0.3
2001	—	6.9±0.7	—	7.4±1.1	—	2.6±0.3	—	7.3±0.2
2002	—	9.0±0.6	—	10.5±1.0	—	3.2±0.4	—	9.2±0.2
H-31								
1997	37.2±2.7	6.7±0.1	108.6±11.8	—	—	—	7.6±0.2	9.0±0.6
1998	35.5±7.4	7.9±0.8	87.2±31.1	4.2±0.8	19.2±6.8	2.1±0.3	9.0±0.5	9.3±1.2
1999	73.2±19.1	7.1±1.4	114.9±17.0	5.8±1.3	31.0±8.1	1.6±0.1	7.7±0.3	10.3±1.3
2000	—	10.0±0.3	—	8.9±0.8	—	2.3±0.3	—	9.2±0.3
SAU-45								
1997	—	—	—	—	—	—	7.7±0.1	—
1998	34.7±2.9	11.7±1.5	85.8±7.9	4.6±0.8	11.5±3.5	2.7±0.5	11.5±1.0	9.1±0.8
1999	50.0±14.2	—	45.5±16.4	—	—	—	—	—
H-22								
1997	—	—	—	—	—	—	—	—
1998	63.1±22.6	20.4±1.9	30.8±3.4	12.0±0.8	16.3±6.4	3.3±0.4	12.8±1.4	10.2±1.0
1999	—	—	—	—	—	—	—	—

Note: Trap material was collected at 30 m water depth.

Table 6. Mean (± standard error) lipid content (percent dry weight) of *Diporeia* exposed to various experimental treatments for a period of 66 days.

		Experimental treatment			
				Sediment	
Day	In situ	Lake water	Sand	H-31	M-45
0 (12 May)	31.8±1.8	31.8±4.6	32.6±3.2	33.1±4.1	29.9±2.6
10 (21 May)	—	24.4±3.6	23.4±1.8	36.4±2.3	28.1±2.4
19 (30 May)	—	26.1±1.2	23.9±4.9	27.4±1.3	24.3±3.1
27 (7 June)	27.4±3.3	—	—	—	—
41 (21 June)	—	28.1±4.0	25.8±2.4	27.4±3.7	26.5±2.5
66 (16 July)	27.1±1.8	22.5±7.0	25.2±2.6	21.3±2.2	22.7±1.5

Note: In situ values were from animals collected at M-45 on the indicated dates.

starved in the laboratory (Gauvin et al. 1989). In these experiments, lipid content declined from 30% to 12% after 120 days and then increased to 18% after 191 days. The increase was attributed to the selective catabolism of non-lipid material (tissue components) after storage lipids were utilized. Weight-specific lipid content may thus increase even though absolute lipid content and total weight may decrease. This possibility seems to be refuted by the consistency in non-lipid weight (relative to length) at the 45 m sites over the time period when lipids increased. Further, absolute lipid content remained stable or actually increased during this period (Fig. 11). Under some circumstances, an increase in lipid content may reflect an interference with lipid degradation or lipid transport processes (Giesy et al. 1988). Accumulated lipids would thus remain unutilized as an energy source during periods of low food availability. The decline in lipid content and lack of mortality during the 66-day food-deprivation experiments indicated, however, that the animals were still able to utilize lipid material as an energy source. The increase and relatively high lipid content at the 45 m sites as populations disappeared suggests that biochemical–physiological changes were occurring in the animals, but the cause and meaning of such changes remain unresolved.

When *Diporeia* were declining, adult fecundity (eggs per brood) was similar to that found in the 1980s when abundances were high. Except in 1994, these young developed and were recruited into the population. Population declines after 1994 occurred because the YOY were not surviving to become juveniles; that is, annual peaks in YOY were generally not followed by increased numbers of juveniles. Eventually, declines in adults resulted from reduced numbers of juveniles rather than adult-specific mortality. Because of higher metabolic and growth rates, YOY are more sensitive

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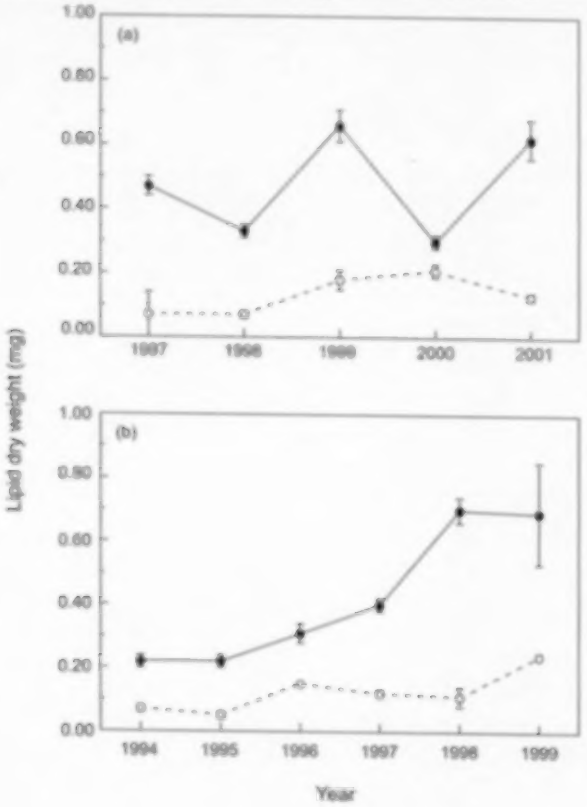
Fig. 11. Mean (± standard error) lipid content (mg) of juvenile (○ - - ○) and adult (● — ●) *Diporeia* spp. at (*a*) M-45 and (*b*) H-31 over the period of declining densities at both sites.



to declines in food levels than adults. In laboratory experiments assessing food competition between YOY and adults, YOY mortality was high at low to medium food regimes, whereas adults were not affected (Hill 1992; Wenngren and Olafsson 2002). Annual fluctuations in *Monoporeia* densities have been attributed to high mortality of YOY because of intraspecific competition for food with adults (Johnson and Wiederholm 1989; Sarvala 1986). Initial declines of juveniles relative to adults at the 45 m sites suggest that food limitation may indeed be a cause of the population decline, at least at these sites. Inconsistent with this premise is that lipid content of juveniles remained high and displayed spring peaks even as numbers decreased.

Nutrient content of the sediments (TOC, BiS, Chl) increased during the study period. Most likely, these increases were a result of dreissenid filtering activities rather than a result of reduced utilization by declining *Diporeia* populations. BiS associated with diatom frustules remains unchanged when consumed by pelagic or benthic grazers, and thus any sediment increase must reflect increased accumulation from the water column. Dreissenids effectively filter fine particulate material from the water column that otherwise would not easily settle; unassimilated material is then deposited in the form of mussel feces and pseudofeces. A 4- to 8-fold increase in sediment concentration of TOC in nearshore Lake Erie after dreissenid colonization was attributed to the accumulation of mussel biodeposits (Howell et al. 1996).

If food limitation was the cause of declines in *Diporeia*, then dreissenid biodeposits must not be available as a nutrition source. Either biodeposits are too refractive to sustain *Diporeia*, or biodeposits are somehow having a negative impact. In laboratory microcosms, *Diporeia* survival was reduced by 25% when exposed to mussel pseudofeces for 90 days (Dermott et al. 2005), so perhaps there is a direct negative response. In contrast, oligochaete densities remained stable between 1993 and 1999, which may reflect an ability to utilize this material as a food source. Whether oligochaetes will persist at these densities remains unclear. In Lake Ontario, where the dreissenid expansion occurred earlier than in Lake Michigan, oligochaete densities have recently declined (Lozano et al. 2001).

Although the loss of *Diporeia* in the Great Lakes has been extensive since *Dreissena* became established, these two taxa do seem to coexist in some areas. In the Finger Lakes, New York, *Diporeia* abundances have not decreased despite an increase in dreissenids over the same time period (Dermott et al. 2005). In Lake Michigan, *Diporeia* continue to be present (although in reduced numbers) at a site <30 m on the western side of the southern basin despite the presence of dreissenids. Upwellings are more frequent on the west side (Plattner et al. 2006), which create conditions of lower temperature and higher productivity that are favorable to *Diporeia*. Lower temperatures associated with upwelling cannot entirely explain the continued presence of *Diporeia* at this shallow, west-side site — populations on the east side disappeared at depths below the thermocline (>30 m) where temperatures were as consistently cold as shallow areas on the west side subject to upwellings. The persistence of *Diporeia* at this site may be temporary, but it does further illustrate the inconsistency associated with temporal and spatial patterns of decline.

Similar to declines of *Diporeia* in the Great Lakes, the related deepwater amphipod *Monoporeia* is also declining in the Baltic Sea (Perus and Bonsdorff 2004). Interestingly, circumstances associated with *Monoporeia*'s decline, as well as uncertainties of potential causes, closely parallel those for *Diporeia*. The decline of *Monoporeia* in most areas was temporally coincident with the invasion of the Baltic by the polychaete *Marenzellaria viridis* (Perus and Bonsdorff 2004). This polychaete is a detritivore and believed to be competing directly with *Monoporeia* for available food resources. Yet the decline in *Monoporeia* was greater in offshore areas (>30 m) than in nearshore areas, even though densities of *Marenzellaria* were greater in the latter (Cederwall et al. 1999). Low oxygen levels have been suggested as the reason for the decline in offshore waters, but others suggest it is food limitation (Cederwall et al. 1999; Kotta and Olafsson 2003). Also, in some parts of the Baltic, the collapse of *Monoporeia* occurred prior to the establishment of *Marenzellaria* (B. Sundelin, Department of Applied Environmental Science, Stockholm University, SE-106 91 Stockholm, Sweden, personal communication).

The decline of *Diporeia* in Lake Michigan, first observed in 1992, continued through 2002. This decline represents a major loss of energy to upper trophic levels. For example, most fish in Lake Michigan are found at depths <90 m

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(Wells 1968). In 1994–1995, mean dry weight biomass (B) of *Diporeia* at depths <90 m was 4.8 g·m^{-2} (Nalepa et al. 2000). Lakewide production (P) at <90 m was thus calculated as 7.7 g·m^{-2} (assuming $P = B \times T^2/10$ (Johnson and Brinkhurst 1971) and a mean temperature (T) of 4 °C). Further assuming that differences in size frequencies and lengths–weights of the *Diporeia* population were minimal between 1994–1995 and 2000, the amount of secondary production lost to fish over this period was 5.1 g·m^{-2}. While this represents a substantial loss, the decline of *Diporeia* has other implications to the fish community besides the loss of a major producer of secondary biomass. *Diporeia* have a higher lipid content and therefore more calories than most other invertebrate prey items. So even if fish switch to other prey, fish bioenergetics will still likely be affected. As evidence, condition and growth of lake whitefish have declined since the loss of *Diporeia* even though alternate prey have been found in their stomachs (Pothoven et al. 2001; Hoyle et al. 2003). A decrease in energy density and (or) lipid content of fish species that serve as prey for the larger piscivores, such as alewife and sculpin, have been attributed to the decline of *Diporeia* (Madenjian et al. 2003; Hondorp et al. 2005). The recent introduction and expansion of quagga mussels into deeper regions of Lake Michigan will likely lead to further declines in *Diporeia* and, hence, further impacts on fish populations.

In summary, features of declining *Diporeia* populations in Lake Michigan were highly variable. Depending on the site, declines in abundances were rapid and apparent in all age classes, or declines were more extended and mostly a result of poor juvenile survival. The former suggests mass mortality in response to perhaps a dreissenid toxic agent, whereas the latter suggests possible food limitation from dreissenid filtering activities. Our quantitative and limited qualitative measures of benthic food inputs, along with observed changes in physiological well-being and laboratory mortality–avoidance experiments, failed to provide conclusive evidence of a cause. Inconsistencies apparent in our results may imply a multitude of causative factors whose relative importance may vary depending on specific environmental conditions. If food limitation is the sole cause, then a nutritional problem not evident from our measures of gross food inputs or physiological well-being is a possibility. Given this, detailed studies of cellular or biochemical indicators may prove worthwhile. For instance, profiles of essential fatty acids (Brett and Muller-Navarra 1997) or functional protein groups (Lopez et al. 2001) in areas with declining and stable populations may show differences specific to nutritional deficiencies or to disease–defense mechanisms. Populations from areas subject to upwelling–downwelling and high–low sedimentation would be of particular interest. By better understanding reasons for *Diporeia*'s decline relative to increased numbers of dreissenids, we may better predict the eventual extent and ultimate consequences of the population loss.

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Changes in seasonal energy dynamics of alewife (*Alosa pseudoharengus*) in Lake Michigan after invasion of dreissenid mussels

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Abstract: The dreissenid mussel invasion of Lake Michigan during the 1990s has been linked to a concomitant decrease in the abundance of the amphipod *Diporeia*. We tracked the seasonal energy dynamics of alewife (*Alosa pseudoharengus*) in Lake Michigan during 2002–2004 and compared our findings with previously published results for years 1979–1981. Adult alewife energy density exhibited a pronounced seasonal cycle during both the pre-invasion and post-invasion periods, with energy density in October or November nearly twice as high as that in early summer. However, on average, adult alewife energy density was 23% lower during the post-invasion period compared with the pre-invasion period. This significant decline in energy density was attributable to decreased importance of *Diporeia* in adult alewife diet. In contrast, energy density of juvenile alewives did not significantly differ between the pre-invasion and post-invasion periods. To attain a weight of 8 kg by age 4, bioenergetics modeling indicated that a Chinook salmon (*Oncorhynchus tshawytscha*) in Lake Michigan would have to consume 22.1% more alewives during the post-invasion period compared with the pre-invasion period.

Résumé : On a relié l'invasion du lac Michigan par les bivalves dreissénidés durant les années 1990 au déclin simultané de l'abondance de l'amphipode *Diporeia*. Nous avons suivi la dynamique énergétique saisonnière des gaspareaux (*Alosa pseudoharengus*) au lac Michigan en 2002–2004 et comparé nos résultats à ceux des années 1979–1981 dans la littérature scientifique. La densité énergétique des gaspareaux adultes suit un cycle saisonnier bien marqué, tant dans les périodes qui précèdent que celles suivent l'invasion; la densité énergétique en octobre ou novembre est presque deux fois plus grande qu'en début d'été. Cependant, en moyenne, la densité énergétique moyenne des gaspareaux adultes est de 23 % plus basse durant la période qui suit l'invasion que durant la période qui la précède. Ce déclin significatif de la densité énergétique s'explique par la diminution considérable des *Diporeia* dans le régime alimentaire des gaspareaux adultes. En revanche, la densité énergétique des jeunes gaspareaux après l'invasion ne diffère pas significativement de celle d'avant l'invasion. Les modèles bioénergétiques indiquent que, pour atteindre une masse de 8 kg à l'âge de 4 ans, les saumons quinnat (*Oncorhynchus tshawytscha*) du lac Michigan doivent consommer 22,1 % plus de gaspareaux durant la période qui suit l'invasion que durant la période qui la précède.

[Traduit par la Rédaction]

Introduction

Although the invasion of lakes and rivers by dreissenid mussels has been shown to have strong influences on the lower food web, soundly demonstrating effects of dreissenid mussel invasions on fish populations has proven to be difficult (Strayer et al. 2004). Few studies have documented clear effects of dreissenid invaders on fish abundance or fish growth. Barriers impeding the detection of dreissenid invader impacts on fish included (*i*) lack of long-term observations on the lower food web, (*ii*) lack of sufficiently long time series of observations on fish abundances or fish growth to discern changes, and (*iii*) complications from changes in other factors during the post-invasion period (Strayer et al. 2004). Moreover, changes in fish growth need to be interpreted in light of changes in fish density (Walters and Post 1993). Fish growth often can be characterized as density-dependent, with growth being inversely related to fish density. For example, the decline in lake whitefish (*Coregonus clupeaformis*) growth and condition in Lake Michigan during the 1990s has been attributed to both a decline in the abundance of the amphipod *Diporeia* and a concomitant in-

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crease in lake whitefish abundance (Pothoven et al. 2001; Madenjian et al. 2002).

To date, effects of dreissenid invasions on the energy dynamics of fish have not been investigated. Yet, a long-term decrease in the energy density of prey fish could result in increased predation on prey fish by piscivorous fish, because the piscivorous fish would need to increase its consumption rate to maintain its growth rate (Rand et al. 1994). Thus, by altering the energy dynamics of a prey fish, a dreissenid invasion could eventually lead to increased consumption of prey fish by piscivorous fish. In aquatic ecosystems where sport fisheries are sustained through stocking of piscivorous fish, substantial increases in consumption of prey fish by piscivorous fish would have management ramifications, including an impetus to reduce stocking rate of the predator (Stewart et al. 1981; Hansen and Holey 2002). Hence, a dreissenid mussel invasion may have potential to perturb aquatic ecosystems all the way to the top-predator level.

Alewife (*Alosa pseudoharengus*) invaded Lake Michigan during the 1940s (Wells and McLain 1973). A major salmonine stocking program was initiated in 1965 to control the alewife population and to establish a sport fishery (Tody and Tanner 1966; Madenjian et al. 2002). The five species of salmonines stocked into the lake included Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*), rainbow trout (*Oncorhynchus mykiss*), lake trout (*Salvelinus namaycush*), and brown trout (*Salmo trutta*). The predominant predator on alewives in Lake Michigan has been Chinook salmon (Madenjian et al. 2002). Based on observations during 1979–1981, Flath and Diana (1985) concluded that adult alewives experience a pronounced seasonal cycle in their energy density, which fluctuated from about 5100 J·g^{-1} (wet weight basis) in June to nearly 9700 J·g^{-1} in late October. During the 1960s and 1970s, *Diporeia* constituted nearly 30% of adult alewife diet in Lake Michigan (Hewett and Stewart 1989). Alewives in Lake Michigan typically do not begin feeding on *Diporeia* until the fall of the second year in the lake (Stewart and Binkowski 1986).

The zebra mussel (*Dreissena polymorpha*) was first observed in Lake Michigan in 1989, and the invader was established in the lake by 1993 (Marsden et al. 1993; Nalepa et al. 1998). The quagga mussel (*Dreissena bugensis*) was first noticed in Lake Michigan in 1997, and this invader was abundant in the lake by 2002 (Nalepa et al. 2001, 2006). Nalepa et al. (2006) documented a decline in *Diporeia* abundance in Lake Michigan during the 1990s and early 2000s, and these researchers have attributed this decline to the dreissenid mussel invasion. Although the mechanisms by which dreissenid mussels negatively affect *Diporeia* remain unidentified, the decrease in *Diporeia* abundance coincided with the dreissenid mussel invasion not only in Lake Michigan, but also in Lakes Huron, Erie, and Ontario (Nalepa et al. 2005, 2006; T. Nalepa, National Oceanic and Atmospheric Administration (NOAA) Great Lakes Environmental Research Laboratory, 2205 Commonwealth Boulevard, Ann Arbor, MI 48105, USA, personal communication).

Quantifying the effects of the dreissenid mussel invasion on alewife energy dynamics would be better facilitated in Lake Michigan compared with most other lakes because (*i*) the benthic macroinvertebrate community has been regularly surveyed in Lake Michigan since 1980 (Nalepa et al. 2006), (*ii*) the seasonal energy dynamics of alewives in Lake Michigan prior to the dreissenid mussel invasion has been well characterized (Flath 1982; Flath and Diana 1985; Stewart and Binkowski 1986), (*iii*) abundance, growth, and condition of alewives in Lake Michigan have been regularly tracked since 1973 (Madenjian et al. 2003, 2005*a*, 2005*b*), and (*iv*) diet of alewives in Lake Michigan has been documented both before and after the dreissenid mussel invasion (Hewett and Stewart 1989; Davis et al. 1997; Hondorp et al. 2005). Because a substantial portion of the food web dynamics in the lake has been explored, the task of isolating effects of the dreissenid mussel invasion on alewives is tractable.

Herein, we measure changes in seasonal energy dynamics of alewives from Lake Michigan following the dreissenid mussel invasion and the accompanying decline in *Diporeia* abundance. To accomplish this primary objective, we characterize the seasonal cycle in alewife energy density during the post-invasion period and then compare the seasonal cycle during the post-invasion period with the seasonal cycle during the pre-invasion period, as determined by Flath and Diana (1985). Secondary objectives of our study include (*i*) measuring the change in alewife lipid content between the pre- and post-invasion periods, (*ii*) determining whether any change in adult alewife energy density between the pre- and post-invasion periods is attributable to density-dependent effects, (*iii*) quantifying the effect of changes in alewife energy density between the pre- and post-invasion periods on food consumption by Chinook salmon, (*iv*) determining the predictability of alewife energy density based on water content, lipid content, and condition, and (*v*) determining whether alewife energy density during 2002–2004 significantly increased as alewife total length increased beyond 90 mm.

Materials and methods

Field sampling

During 2002–2004, alewives were caught in bottom trawls and gill nets from a variety of locations in Lake Michigan. During September and October 2002–2003, alewives were captured during the lakewide survey of the Lake Michigan fish community conducted by the Great Lakes Science Center (GLSC). This GLSC lakewide survey has been performed each fall since 1973. The basic unit of sampling for the GLSC survey was a 10 min tow using a bottom trawl (12 m headrope and 13 mm stretched-mesh liner) dragged on depth contour during daylight hours (Hatch et al. 1981; Madenjian et al. 2005*a*, 2005*b*). Sampling depths ranged from 9 to 110 m. The complete survey included transects off these seven ports: Manistique (Michigan), Frankfort (Michigan), Ludington (Michigan), Saugatuck (Michigan), Waukegan (Illinois), Port Washington (Wisconsin), and Sturgeon Bay (Wisconsin) (Fig. 1). Owing to mechanical problems aboard the vessel and time constraints, tows at Manistique were not performed in 2002. For each combination of port and year, an attempt was made to collect 100 large (>120 mm in total length (TL)) and 100 small (≤120 mm TL) alewives. A cutoff length of 120 mm TL was employed to match the classification system used by Stewart et al. (1981, 1983) to develop bioenergetics models for Lake Michigan salmonines. Fish were separated by size category, bagged with water, frozen, and transported to the GLSC laboratory in Ann

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Fig. 1. Map of Lake Michigan, including locations of sampling sites. Solid circles denote locations of sampling sites for the US Geological Survey Great Lakes Science Center bottom trawl survey. Open squares denote locations of sites sampled by the National Oceanic and Atmospheric Administration Great Lakes Environmental Research Laboratory researchers. Open triangles denote locations of sites sampled by Illinois Natural History Survey and Illinois Department of Natural Resources researchers.

Arbor (Michigan), where they were stored in a freezer at −30 °C until processing.

In Lake Michigan in the vicinity of Muskegon (Michigan) (Fig. 1), alewives were caught during April through November 2003–2004 using a semi-balloon bottom trawl (7.8 m headrope with 13 mm stretch mesh liner). Trawl tows were conducted during daylight hours at depths ranging from 10 to 90 m, depending on seasonal inshore–offshore movements of alewives. All sampling was performed by NOAA Great Lakes Environmental Research Laboratory researchers. For each combination of year and month, an attempt was made to collect 100 large and 100 small alewives. Again, fish were separated by size class, bagged with water, frozen, and transported to the GLSC laboratory.

From the Illinois waters of Lake Michigan near Waukegan (Fig. 1), alewives were caught during April through October 2003–2004 by Illinois Department of Natural Resources and Illinois Natural History Survey personnel. During April and May, graded-mesh gillnets were fished overnight at various depths between 10 and 100 m. During June through October, alewives were captured monthly using a bottom trawl (4.9 m headrope with 13 mm stretched-mesh liner) fished during daylight hours at depths ranging from 3 to 10 m. All alewives were sorted by size class and immediately placed on

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ice. Upon return to the laboratory in Zion (Illinois), up to 100 large and 100 small individuals were frozen in water each month and then transported to the GLSC laboratory.

Laboratory processing of samples

After thawing in the laboratory, each alewife's TL was measured to the nearest millimetre, and each alewife was weighed to the nearest 0.1 g. Up to five 20-fish composites were formed for each combination of year, month, port, and size class. Each composite was then homogenized in a blender, and between 40 and 120 g of the homogenate was placed in a glass jar. Each jar was sealed with aluminum foil, capped, and kept frozen at –30 °C until time of energy density or lipid content determinations.

To determine energy density, about 35 g of the homogenate was dried to a constant weight in a drying oven at 70 °C; drying typically required about 3 days. The dried tissue was ground using a mortar and pestle, and then 1 g of the dried sample was combusted in a Parr 1261 isoperibol calorimeter. All energy densities were reported on a wet weight basis.

To estimate the variability in our energy density determinations from an alewife composite sample, we determined energy density of three replicates from each of 10 samples. The coefficient of variation averaged 1.03% over the 10 samples. Flath (1982) reported an average coefficient of variation of 1.05% for his replicate values of energy density determinations. Thus, precision in the estimates of alewife energy density was very similar between our study and that of Flath and Diana (1985).

For large alewives, Flath and Diana (1985) removed the contents of the stomachs before determining energy density, whereas we included the stomach contents in our energy density determinations. However, this difference in processing had a practically negligible effect on comparability of energy density between the two studies, because stomach contents of large alewives from Lake Michigan represent only about 1% of their body weight (Davis et al. 1997; S.A. Pothoven, unpublished data). For example, the food found in the stomachs of large alewives caught near Muskegon during August 2004 comprised 1.36% of their total body weight on average. Coupling our estimate of large alewife energy density (at Muskegon during August 2004) with published values for the energy density of the prey found in the stomachs, we estimated a factor of 1.008 to correct our energy density estimate for direct comparison with an energy density estimate by Flath and Diana (1985). Given the extremely low value of this correction factor, we opted not to apply it to our estimates of energy density.

To determine lipid content, the procedure outlined by Schmidt and Hesselberg (1992) was followed. Lipids were extracted from the homogenate using petroleum ether and ethyl acetate as solvents. Percent extractable lipid was determined by evaporating 1 mL of extract and weighing the residue (Hesselberg et al. 1990). All lipid contents were reported on a wet weight basis.

Data analysis

To compare alewife energy density during 2002–2004 with alewife energy density during 1979–1981, we first calculated mean energy density during the 2002–2004 period for each combination of month and alewife size category. Data from all years (2002–2004) and all ports were pooled for these calculations. For each combination of month and alewife size category, we also calculated the average day of capture during the month. We assigned mean energy density to the average day of capture for the month. In addition, the 95% confidence interval was calculated for each mean energy density. Next, we plotted the mean energy densities, with corresponding 95% confidence intervals, from the 2002–2004 period together with the alewife energy density schedules developed by Stewart and Binkowski (1986) and Hewett and Johnson (1992), largely based on 1979–1981 data from Flath and Diana (1985). For both small and large alewives, we paired monthly means of energy density from the 2002–2004 period with corresponding values from the energy density schedule based on 1979–1981 data and then performed a *t* test for paired comparisons to determine if mean energy density significantly changed between the 1979–1981 and 2002–2004 periods. Stewart and Binkowski (1986) developed their energy density schedule for small alewives by using data for only young-of-the-year alewives during the fall months. However, an age–length key, presented in Madenjian et al. (2005*b*), indicated that the alewives used to form five composite samples from November 2004 were most likely yearlings. Therefore, to better compare the energy densities from 2002–2004 with the energy density schedule developed by Stewart and Binkowski (1986), these five samples were not included in this analysis.

We were justified in pooling data across years 2002–2004 and across all ports sampled during 2002–2004 because (*i*) energy density did not vary significantly across the years, and (*ii*) Stewart and Binkowski (1986) also pooled data across years and ports in developing their energy density schedules for alewives. For both small and large alewives, mean energy density of fish caught during GLSC fall surveys did not significantly differ between 2002 and 2003 (two-sample *t* tests, $P > 0.05$). Similarly, neither alewives from Muskegon nor alewives from Waukegan (caught by State of Illinois researchers) differed significantly in energy content between years 2003 and 2004 (two-sample *t* tests, $P > 0.05$). In addition, alewife energy density at Muskegon and Waukegan appeared to be representative of the lake, because mean energy density of alewives at Muskegon and Waukegan during September and October of 2003 did not significantly differ from mean energy density of alewives caught in the GLSC lakewide survey during 2003 (two-sample *t* tests, $P > 0.05$). Alewives used in the Flath and Diana (1985) study were caught near Saugatuck, Port Sheldon (Michigan), and Grand Haven (Michigan) during 1979–1981. Stewart and Binkowski (1986) believed that their energy density schedules were representative of the lake, because their energy density schedules were very similar to ones derived from observations by Yeo (1978) for alewives caught in Wisconsin waters of Lake Michigan during the 1970s.

To compare alewife lipid content during 2002–2004 with alewife lipid content during 1979–1981, we first calculated mean lipid content and its corresponding 95% confidence interval of large alewives by month during 2002–2004. Data were pooled across years and ports in calculating these monthly means. We then plotted monthly means with 95% confidence intervals together with the monthly means for

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alewife lipid content presented by Flath and Diana (1985) from observations during 1979–1981. In addition, a *t* test for paired comparisons was performed to determine if lipid content of large alewives significantly changed between the 1979–1981 and 2002–2004 periods. Comparison of lipid content of small alewives between the two time periods was not conducted, because lipid content data for small alewives during 1979–1981 were not reported by Flath and Diana (1985).

To compare the diet composition of adult alewives of Lake Michigan between the pre-invasion and post-invasion periods, we surveyed the literature. Hewett and Stewart (1989) integrated the data from several diet studies on Lake Michigan alewives performed during the 1960s and 1970s to arrive at an annual diet schedule for Lake Michigan adult alewives; this diet schedule was then used in their bioenergetics model applications. Their diet schedule represented data from both the eastern and western sides of the lake. Using the Hewett and Stewart (1989) diet schedule, we averaged the proportion of each of the various components in the diet across all seasons to compute an annual average diet composition for adult alewives in Lake Michigan during the pre-invasion period. Davis et al. (1997) characterized the diet of adult alewives caught in Lake Michigan near Saugatuck, Port Washington, and Sturgeon Bay during spring and fall 1995. Similarly, Hondorp et al. (2005) characterized the diet of adult alewives caught in Lake Michigan near Muskegon and St. Joseph (Michigan) during spring, summer, and fall 2000–2001. Using data from these two studies, we averaged the proportion of each of the components in the diet across seasons and locations to calculate an annual average diet composition for adult alewives in Lake Michigan during the post-invasion period. We calculated diet compositions on a wet weight basis. Using these calculated annual average diet compositions, we compared the proportion of *Diporeia* in adult alewife diet during the pre-invasion with that during the post-invasion period. In addition, we used the calculated annual average diet compositions, as well as the energy densities for each of the diet components as reported by Hewett and Stewart (1989), to estimate the energy density of the food of Lake Michigan adult alewives during both the pre-invasion and post-invasion periods.

To determine the reliability of predicting alewife energy density based on a correlate, we conducted simple linear regression analyses of alewife energy density as a function of percent water, lipid content, and condition. To use condition in the regression analysis, we calculated Fulton's condition K (equal to (weight $\times 10^5$) $\times$ TL^{-3}) for each of the 20 alewives in the composite sample and then calculated the average K for the sample; weight is expressed in grams and TL is expressed in millimetres. The percent variation in alewife energy density explained by the predictor was calculated for each of the three regressions. Data from all 220 alewife composites were included in our first set of regression analyses. In our second set of regression analyses, we divided the data into one set for small alewives and one set for large alewives. We then performed a simple linear regression of energy density as a function of each of the three predictor variables for both small and large alewives.

To corroborate our assessment of the effect of the dreissenid mussel invasion on energy density of adult alewives in Lake Michigan, we first calculated the decrease in adult alewife K between the 1979–1994 and 1995–2004 periods using the long-term data from the GLSC fall lakewide surveys. For this analysis, we considered adult alewives to be those of spawner size (TL $\geq$ 150 mm) (O'Gorman et al. 2004; Madenjian et al. 2005*a*). Condition of age-2 and older alewives in Lake Michigan decreased by 14% between the 1984–1994 and 1995–2001 periods (Madenjian et al. 2003). We added data from years 1979–1983 and 2002–2004 to the data used in their study to bracket all of the years encompassed by our comparison, calculated mean condition of adult alewives for each year during 1979–2004, and then averaged annual means to generate grand means for the 1979–1994 and 1995–2004 periods. Next, we substituted these two grand means into the regression equation for energy density of large alewives as a function of condition to estimate mean energy density of adult alewives in the fall during the 1979–1994 and 1995–2004 periods. The percent change in energy density between the two time periods was then calculated. This calculated percent change in energy density was then compared with the percent change in energy density calculated by direct comparison of the energy density schedule for large alewives developed by Stewart and Binkowski (1986) and our energy density schedule for large alewives from 2002–2004 data. More specifically, we averaged the eight monthly means for energy density of large alewives to arrive at an overall mean energy density for large alewives during 2002–2004. We also averaged the eight corresponding values on the Stewart and Binkowski (1986) energy density schedule for large alewives to generate an overall mean energy density for large alewives during the 1979–1981 period. Then, the percent change in mean energy density between the two time periods was calculated. Madenjian et al. (2003) used change-point regression analysis to show that a stepwise decline in alewife condition occurred in 1995. We applied change-point regression analysis to the extended time series, including years 1979–2004, for mean condition of adult alewives to confirm that the drop in alewife condition did occur in 1995.

To determine whether a change in adult alewife energy density was attributable to density-dependent effects, we compared mean abundance (expressed as kg·ha^{-1}) of adult alewives in Lake Michigan during 1979–1981 with that during 2002–2004, using the long-term data from the GLSC bottom trawl survey (Madenjian et al. 2005*b*). In addition, we computed the correlation coefficient between mean K for adult alewives and adult alewife annual abundance, using the 1979–2004 data. Then, we determined whether the correlation coefficient was significantly different from zero ($P > 0.05$). This test was performed to ascertain whether adult alewife condition showed a significant density-dependent response over the range of densities observed during 1979–2004.

Flath (1982) observed neither an increasing nor decreasing trend in alewife energy density as alewife TL increased beyond 90 mm during 1979–1981. To determine whether this same pattern was present during 2002–2004, we performed a simple linear regression of alewife energy density as a function of alewife TL $\geq$ 90 mm. Based largely on the Flath (1982) and Flath and Diana (1985) data, Stewart and Binkowski (1986) concluded that energy density showed no

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further increase as alewife age increased beyond 2 years. Thus, to characterize the seasonal energy dynamics of large alewives from Lake Michigan, Stewart and Binkowski (1986) relied on determinations of energy density for age-2 and older alewives only. To estimate the percentage of age-2 and older alewives in the set of large alewives used in our study, we applied an age–length key, taken from Madenjian et al. (2005*b*), to the length–frequency distribution of large alewives used in our study.

Bioenergetics modeling

We used the bioenergetics model for Chinook salmon originally formulated by Stewart (1980) and Stewart et al. (1981), and later refined by Stewart and Ibarra (1991), to determine the effect of long-term changes in alewife energy density on consumption of alewives by Chinook salmon. The same water temperature regime and diet composition schedules used by Stewart and Ibarra (1991) were used in our simulations. Chinook salmon weight at age in Lake Michigan trended neither upward nor downward during 1983–2003 (Peeters and Royseck 2004). The growth trajectory based on weight-at-age data for 1983 represented a typical growth trajectory for Chinook salmon in Lake Michigan during the post-1982 period (Szalai 2003); we used this trajectory as inputs to the bioenergetics model for our simulations. According to this trajectory, weights at time of stocking, age 1, age 2, age 3, and age 4 were 4.5 g, 586 g, 2.557 kg, 5.463 kg, and 7.865 kg, respectively. Using the bioenergetics modeling software by Hanson et al. (1997), Chinook salmon growth and consumption was simulated from time of stocking to age 4 both under the alewife energy density schedules developed by Stewart and Binkowski (1986) and under the alewife energy density schedules from our 2002–2004 data. To generate our schedules, we assigned the mean monthly energy density to the average day of capture for the month and then linearly interpolated among the eight monthly means.

Results

Energy density of small (≤120 mm TL) alewives in April, August, October, and November was higher during the post-invasion period than during the pre-invasion period (Fig. 2*a*). In May, June, July, and September, energy density of small alewives during 1979–1981 was higher than the corresponding value from the 2002–2004 schedule. Confidence intervals about the monthly means for 2002–2004 overlapped the corresponding values from the 1979–1981 schedule in April, August, September, and November (Fig. 2*a*). Averaging the eight monthly means from 2002–2004 yielded a grand mean of 4.556 kJ·g^{-1}, and averaging the eight corresponding points from the 1979–1981 schedule yielded a grand mean of 4.661 kJ·g^{-1}. Mean energy density of small alewives during post-invasion period was not significantly different from mean energy density of small alewives during the pre-invasion period (mean difference = 0.104 kJ·g^{-1}; t = 0.46, df = 7, P = 0.6587).

Energy density of large (>120 mm TL) alewives during the pre-invasion period exceeded large alewife energy density during post-invasion period over all months between April and November (Fig. 2*b*). Only in June did the confidence interval about the monthly mean from the 2002–2004 schedule overlap with the corresponding value from the 1979–1981 schedule. The average of the eight monthly means for 2002–2004 was 5.413 kJ·g^{-1}, whereas the average of the eight corresponding points from the 1979–1981 schedule was 7.030 kJ·g^{-1}. Thus, large alewife energy density was 23.0% lower during the post-invasion period compared with the pre-invasion period. Mean energy density of large alewives was significantly higher during the pre-invasion period than during the post-invasion period (mean difference = 1.617 kJ·g^{-1}; t = 6.95, df = 7, P = 0.0002).

Lipid content of large alewives was higher during the pre-invasion period than during the post-invasion period in each of the 6 months for which data from 1979–1981 were available (Fig. 3). Moreover, 95% confidence intervals about the monthly means for 2002–2004 did not overlap with the corresponding monthly means for 1979–1981 in any of the 6 months. Mean lipid content over the 6 months (depicted in Fig. 3) was 9.1% during 1979–1981, but only 3.9% during 2002–2004; this difference was significant (mean difference =

Fig. 2. Energy density of (*a*) small (≤120 mm total length, TL) and (*b*) large (>120 mm TL) alewives (*Alosa pseudoharengus*) in Lake Michigan during 1979–1981 (solid line) and during 2002–2004 (solid circles). Energy density schedule during 1979–1981 was taken from Stewart and Binkowski (1986) and Hewett and Johnson (1992). Bars about each point represent the 95% confidence interval about the mean. Energy density is expressed on a wet weight basis.

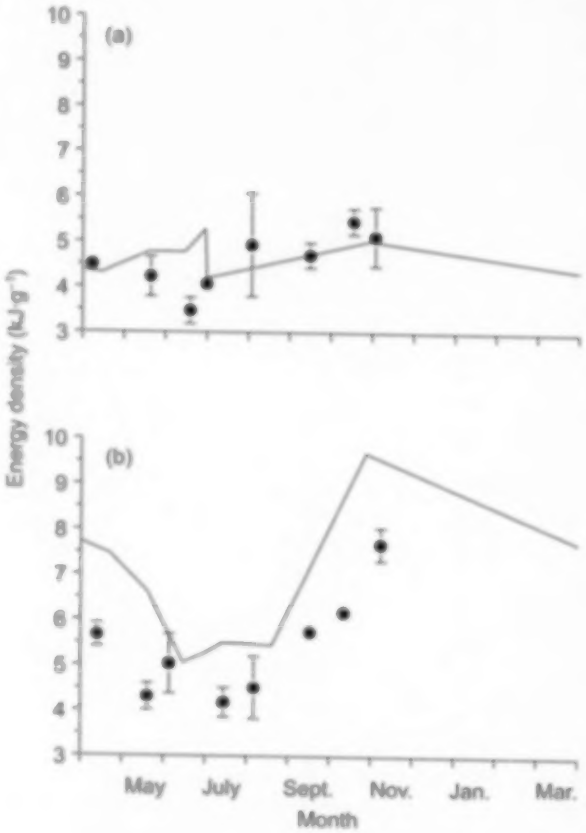

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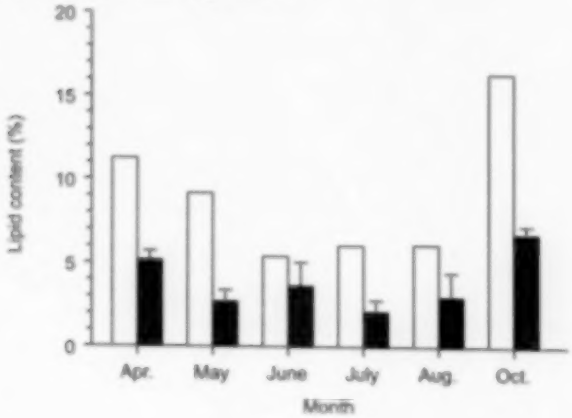
Fig. 3. Mean lipid content of large (>120 mm total length) alewives (*Alosa pseudoharengus*) in Lake Michigan during 1979–1981 (open bars) and during 2002–2004 (solid bars). Lipid content during 1979–1981 was taken from Flath and Diana (1985). Error bars represent 95% confidence interval. Lipid content is expressed on a wet weight basis.



5.1%; $t = 4.49$, df = 5, $P = 0.0064$). It should be pointed out that mean lipid content of large alewives in November during 2002–2004 was 10.7% (Table 1). However, even considering the relatively high lipid content observed during November 2002–2004, lipid content of large alewives in Lake Michigan decreased by roughly 50% between the two time periods.

Lipid content of small alewives ranged from 1.7% in June to 5.6% in November during the post-invasion period (Table 1). In general, both lipid content and energy density of large alewives were higher than lipid content and energy density of small alewives.

Proportions of cladocerans, copepods, *Mysis*, and *Diporeia* in Lake Michigan adult alewife diet during the pre-invasion period were 0.26, 0.34, 0.11, and 0.29, respectively. Proportions of cladocerans, copepods, *Mysis*, and *Diporeia* in Lake Michigan adult alewife diet during the post-invasion period were 0.35, 0.36, 0.17, and 0.12, respectively. Energy densities of cladocerans, copepods, *Mysis*, and *Diporeia* have been reported as 1.674, 2.300, 4.604, and 4.185 kJ·g^{-1}, respectively, on a wet weight basis (Hewett and Stewart 1989). Thus, the energy densities of the food of adult alewives in Lake Michigan during the pre-invasion and post-invasion periods were 2.939 and 2.699 kJ·g^{-1}, respectively.

Percent water was better correlated with energy density than with either lipid content or condition (Table 2; Fig. 4). Percent water and lipid content were very good to excellent predictors of alewife energy density. Percent water accounted for 94%, 97%, and 95% of the variation in energy density for small alewives, large alewives, and alewives of both sizes, respectively (Table 2). Lipid content explained 86%, 96%, and 91% of the variation in energy density for small alewives, large alewives, and alewives of both sizes, respectively. Condition was a fairly reliable indicator of energy density of large alewives, as condition explained 75% of the variation in energy density (Table 2; Fig. 4). However, the reliability of condition as a predictor of energy density was lower for small alewives or for alewives of both sizes.

Examination of the GLSC long-term series of observations on condition of adult alewives in Lake Michigan corroborated results from our direct comparison of energy density of large alewives between the pre- and post-invasion periods. Change-point regression analysis applied to this long-term series identified 1995 as a change-point year (Fig. 5). Further, mean condition did not show a significant trend during 1979–1994 (t test; $t = 1.89$, df = 13, $P = 0.0809$) or during 1995–2004 (t test; $t = 0.81$, df = 8, $P = 0.4393$). Mean condition of adult alewives was significantly higher during 1979–1994 than during 1995–2004 (t test; $t = 6.87$, df = 23, $P < 0.0001$). Residuals from these statistical analyses were not significantly autocorrelated (portmanteau test from Box and Jenkins (1976); $P > 0.05$). Mean condition decreased from 0.83 during 1979–1994 to 0.73 during 1995–2004 (Fig. 5). Substitution of these two means into the regression equation for large alewives from Table 2 yielded predictions of alewife energy density of 7.215 and 5.650 kJ·g^{-1} during the pre- and post-invasion periods, respectively. Thus, energy density of large alewives was predicted to decrease 21.7% between the two time periods, based on long-term series of observations on adult alewife condition and use of the regression equation to predict energy density from condition. Results from our direct comparison showed that energy density of large alewives decreased 23.0% between the pre- and post-invasion periods. Given the amount of variability about the regression line for energy density as a function of condition (Fig. 4c), this prediction of changes in energy density based on long-term trends in adult alewife condition was reasonably close to the change in large alewife energy density estimated by our direct comparison of observations on energy density between the two time periods.

The decline in energy density of large alewives between 1979–1981 and 2002–2004 was not due to higher abundance of alewives during the 2002–2004 period. Based on the GLSC lakewide fall surveys, average adult density of alewives was 11.8 kg·ha^{-1} during 1979–1981 and 9.1 kg·ha^{-1} during 2002–2004. Additionally, the correlation coefficient between mean K of adult alewives and adult alewife abundance was not significantly different from zero ($r = -0.36$; $t = -1.76$; df = 21; $P = 0.0935$).

Alewife energy density during the post-invasion period did not significantly change as alewife TL increased beyond 90 mm (slope = 0.0054 kJ·mm^{-1}; $t = 1.04$, df = 160, $P = 0.2998$). Based on application of the age–length key to the length–frequency distribution, 99.5% of the large alewives used in our study were age 2 or older.

According to the results of the bioenergetics modeling, long-term changes in the energy density schedule for alewives could have a substantial effect on the amount of alewives consumed by a Chinook salmon in Lake Michigan. Based on the energy density schedules for alewives during the pre-invasion period (as depicted in Fig. 2), a Chinook salmon would consume 38.523 kg of alewives to attain a size of 7.865 kg after spending 4 years in the lake. Based on the post-invasion energy density schedule (also depicted in Fig. 2), a Chinook salmon would consume 47.028 kg of alewives to attain the same size while spending 4 years in the

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Table 1. Mean energy density and mean lipid content of small (≤120 mm total length, TL) and large (>120 mm TL) alewives (*Alosa pseudoharengus*) from Lake Michigan, by month, during 2002–2004.

	Small alewives				Large alewives			
Month	*N*	Mean capture day	Mean energy density (kJ·g^{-1})	Mean lipid content (%)	*N*	Mean capture day	Mean energy density (kJ·g^{-1})	Mean lipid content (%)
April	6	8	4.493 (0.062)	4.0 (0.2)	7	13	5.665 (0.105)	5.2 (0.2)
May	16	21	4.223 (0.208)	3.3 (0.4)	17	20	4.312 (0.140)	2.7 (0.3)
June	4	19	3.471 (0.090)	1.7 (0.3)	7	5	5.035 (0.267)	3.7 (0.6)
July	6	1	4.059 (0.065)	2.5 (0.1)	11	15	4.184 (0.149)	2.1 (0.3)
August	3	3	4.926 (0.265)	4.4 (0.3)	7	6	4.514 (0.282)	3.0 (0.6)
September	11	15	4.703 (0.124)	3.3 (0.2)	57	16	5.741 (0.083)	5.5 (0.2)
October	12	17	5.458 (0.129)	5.1 (0.2)	32	11	6.172 (0.080)	6.8 (0.2)
November	7	2	5.120 (0.266)	5.6 (0.5)	12	7	7.680 (0.164)	10.7 (0.4)

Note: Standard error is shown in parentheses. *N* is the number of observations; each observation represents a determination from a 20-fish composite. Mean capture day refers to the average day of capture for the month. Energy density and lipid content are expressed on a wet-weight basis.

Table 2. Simple linear regression coefficients for energy density (kJ·g^{-1}) as a function of percent water, lipid content, and Fulton's condition.

Predictor	Grouping	α	β	r^2
Percent water (%)	Small alewife	30.4602	−0.3243	0.94
	Large alewife	33.7474	−0.3705	0.97
	Both sizes	31.0678	−0.3342	0.95
Lipid content (%)	Small alewife	3.1482	0.3797	0.86
	Large alewife	3.4249	0.4062	0.96
	Both sizes	3.2795	0.4101	0.91
Fulton's condition (*K*)	Small alewife	−1.0077	8.6944	0.39
	Large alewife	−5.8073	15.6554	0.75
	Both sizes	−3.7265	12.7857	0.64

Note: Small (≤120 mm total length, TL) alewife (*Alosa pseudoharengus*) regressions are based on 70 samples and large (>120 mm TL) alewife regressions are based on 150 samples. Energy density and lipid content are expressed on a wet weight basis. α, regression line intercept; β, regression line slope; r^2, proportion of variation in energy density explained by the predictor variable.

lake. Thus, alewife consumption by Chinook salmon would have to increase 22.1% to compensate for the decrease in alewife energy density between the pre- and post-invasion periods while maintaining the same growth.

Discussion

In conjunction with alewife diet studies, our analyses indicated that energy density of large alewives in Lake Michigan has decreased by more than 20% as a consequence of the dreissenid mussel invasion and the accompanying decrease in *Diporeia* abundance. Our direct comparison of data from the pre-invasion period with that from the post-invasion period showed that energy density of large alewives in the lake decreased by 23% between the two time periods. Furthermore, our analysis of the long-term trends in condition of adult alewives from the lake suggested that the decrease in energy density occurred during the mid 1990s, just after establishment of a zebra mussel population throughout Lake Michigan. Diet data for alewives in Lake Michigan also supported the contention that the dreissenid mussel invasion led to the decline in large alewife energy density. *Diporeia* accounted for 29% of the adult alewife diet in Lake Michigan during the pre-invasion period, whereas *Diporeia* represented only 12% of the adult alewife diet in Lake Michigan during the post-invasion period. Therefore, the importance of *Diporeia* in alewife diet in Lake Michigan decreased substantially between the 1960–1994 and 1995–2004 periods. Moreover, large alewife energy density at Muskegon was higher than that at St. Joseph, and Hondorp et al. (2005) attributed the difference to a greater proportion of *Diporeia* in the alewife diet at Muskegon. *Diporeia* is relatively high in lipid content compared with other invertebrates, and a decrease in its importance in the diet of large alewives would be expected to lead to decreases in both lipid content and energy density (Madenjian et al. 2000*a*). Furthermore, based on our analyses, the hypothesis that density-dependent effects were responsible for the decrease in adult alewife energy density between the pre- and post-invasion periods could be soundly dismissed. Finally, as previously mentioned, the substantial decline in *Diporeia* abundance in Lake Michigan during the 1990s has been attributed to the dreissenid mussel invasion (Nalepa et al. 2005, 2006).

Our finding that energy density of small alewives did not substantially change between the pre- and post-invasion periods further supported the contention that the dreissenid mussel invasion, along with the accompanying decline in *Diporeia* abundance, were responsible for decreased energy density of large alewives. Alewives in Lake Michigan typically do not begin to feed on *Diporeia* at a substantial rate

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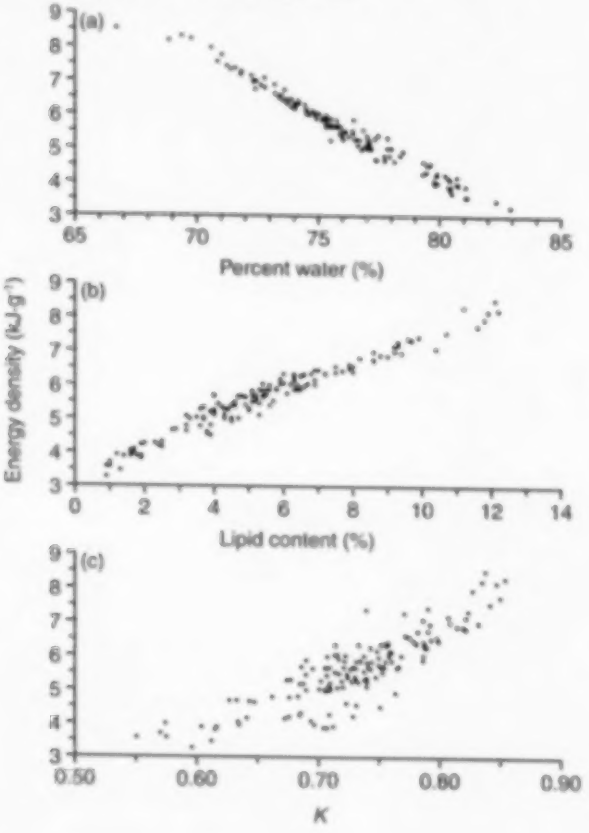
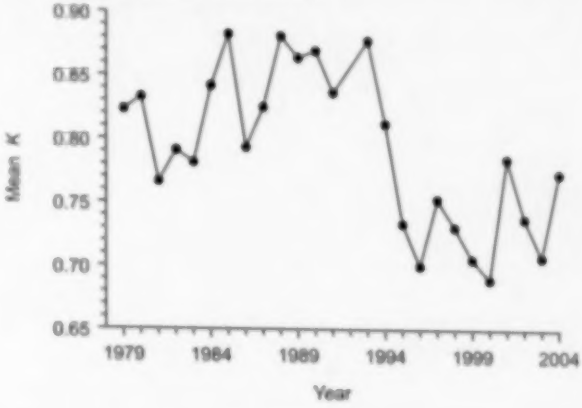
Fig. 4. Scatter plots of energy density of large (>120 mm total length) alewives (*Alosa pseudoharengus*) in Lake Michigan during 2002–2004 as a function of their percent water, lipid content, and condition (Fulton's *K*). Each point represents a determination from a 20-fish composite sample. Condition was averaged over the 20 fish forming the composite. Energy density and lipid content are expressed on a wet weight basis.



until the fall of their second year in the lake (Stewart and Binkowski 1986). Because small alewives do not utilize *Diporeia* as a food source to any sizeable degree, a decrease in the abundance of *Diporeia* would not be expected to affect the energy density of small alewives.

Large alewives appeared to exhibit a threshold response to decreasing levels of *Diporeia* abundance, because the importance of *Diporeia* in adult alewife diet and adult alewife condition appeared to rapidly drop once abundance of *Diporeia* fell below a certain level. Also, alewife condition remained at a low level as *Diporeia* abundance continued to decline following 1995. *Diporeia* density in southern Lake Michigan decreased from 5175 individuals·m^{-2} in 1992–1993 to 1936 individuals·m^{-2} in 1997–1998 and then further decreased to 1438 individuals·m^{-2} in 2002–2003 (Nalepa et al. 2006); the threshold level would be between the 1992–1993 and 1997–1998 values. In an analogous case, once white perch (*Morone americana*) attained a certain level of abundance in Lake Erie, recruitment of white bass (*Morone chrysops*) immediately dropped and recruitment has remained low since 1982

Fig. 5. Mean condition (Fulton's *K*) of spawner-size (≥150 mm total length) alewives (*Alosa pseudoharengus*) in Lake Michigan, 1979–2004. Data from the US Geological Survey Great Lakes Science Center bottom trawl survey.



(Madenjian et al. 2000*b*). White perch invaded Lake Erie during the 1970s, became well established in the lake by 1982, and their abundance continued to increase from 1982 to 1991. As the impacts of invaders are further explored in the upcoming years, we would expect more documented examples of a threshold response on the part of the native or naturalized population to the invasion. Because these threshold responses are highly nonlinear, the problem of determining the effects of an invasion on the fish community is rendered more complex by having to consider both linear and threshold responses.

Apparently, both the proportion of *Diporeia* in the diet and the feeding rate of adult alewives in Lake Michigan declined between the pre- and post-invasion periods. As previously mentioned, the proportion of *Diporeia* in adult alewife diet declined from 0.29 to 0.12 between the two time periods. We calculated that the energy density of the food of adult alewives in Lake Michigan declined from 2.939 to 2.699 kJ·g^{-1} between the two time periods; this decline represented an 8% drop in food energy density. In addition, average weight at age of adult alewives decreased approximately 20% between the 1984–1994 and 1995–2001 periods (Madenjian et al. 2003). A reduction in growth is typically caused by a reduction in feeding rate (Stewart and Binkowski 1986). Lipid content is directly proportional to energy density, and lipid content is dependent on both the lipid content of the food and feeding rate (Madenjian et al. 2000*a*). Therefore, the decline in adult alewife energy density between the pre- and post-invasion periods was likely due to both the decreased proportion of *Diporeia* in adult alewife diet and an overall reduction in feeding rate of adult alewives.

Although the simplest and most obvious explanation for the reduced importance of *Diporeia* in adult alewife diet in Lake Michigan was the decrease in *Diporeia* abundance during the 1990s, the possibility that other factors were involved with the reduced importance of *Diporeia* in adult alewife diet cannot be completely ruled out. Mean depth of alewives caught in GLSC bottom trawls from the annual fall survey trended neither upward nor downward during the

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1990s (C. Madenjian, unpublished data), so alewife spatial distribution apparently did not change during the 1990s. Similarly, based on sampling with Ponar grabs, no apparent changes in *Diporeia* behavior during the 1990s were evident (T. Nalepa, NOAA Great Lakes Environmental Research Laboratory, 2205 Commonwealth Boulevard, Ann Arbor, MI 48105, USA, personal communication). Nevertheless, perhaps changes in some aspects of alewife or *Diporeia* behavior, which were undetected by surveys in the lake, resulted in reduced availability of *Diporeia* to alewives. However, the most parsimonious explanation for decreased importance of *Diporeia* in adult alewife diet during the late 1990s remains decreased *Diporeia* abundance.

Despite the overall decrease in energy density of large alewives in Lake Michigan between the pre- and post-invasion periods, energy density of large alewives exhibited a pronounced seasonal cycle during both time periods. The trough of the cycle occurred during early summer and the peak of the cycle was during the fall, when energy density was nearly twice as high as the summer minimum value. Stewart and Binkowski (1986) attributed the seasonal cycle in large alewife energy density to the highest feeding rates occurring during the fall, low feeding rates during the winter, increased feeding rates during the spring, and then a decrease in feeding rates in early summer prior to spawning. The dreissenid mussel invasion, and its subsequent negative effect on *Diporeia* abundance, did not appear to disrupt this seasonal pattern in feeding rate. The last sampling date of the calendar year included in the Flath and Diana (1985) study was 27 October, and Stewart and Binkowski (1986) speculated that the peak energy density of large alewives may occur in November or December rather than in late October. Our study results suggested that energy density of large alewives may continue to increase into November. Additional sampling will be required to determine the precise time of the year at which peak energy density of large alewives occurs.

Although the average TL of large alewives used in energy density determinations by Flath and Diana (1985) slightly exceeded the average TL of large alewives used in our study (165 vs. 155 mm), the contribution of this size difference toward explaining the observed difference in energy density between the pre- and post-invasion periods was negligible. We found that alewife energy density did not significantly increase as alewife TL exceeded 90 mm. Moreover, practically all of the large alewives used in our study were age 2 or older, and so our results were directly comparable with the results from Flath and Diana (1985). We also point out that even if adult alewife energy density did continue to increase with increasing alewife size, the observed difference in energy density between the pre- and post-invasion periods would still be attributable to the dreissenid mussel invasion. Madenjian et al. (2003) documented a decrease in mean length at age and mean weight at age in alewives from Lake Michigan during the 1990s, and they ascribed this decrease in growth to decreased abundance of *Diporeia*. Therefore, the presence of smaller adult alewives in Lake Michigan during 2002–2004 compared with 1979–1981 was probably due to the dreissenid mussel invasion.

Because Chinook salmon size at age in Lake Michigan has remained relatively stable over the past 20 years (Peeters and Royseck 2004), our bioenergetics modeling results indicated that Lake Michigan Chinook salmon have compensated for the decrease in adult alewife energy density during the 1990s by increasing their consumption rates so that growth rate has not changed. Our model simulations were based on the assumption that Chinook salmon activity did not change between the pre- and post-invasion periods. Such an assumption may be reasonable, given that Chinook salmon appear to be an accomplished predator on clupeids (Healey 1991).

To better manage the salmonine fisheries of Lake Michigan and to better understand the role of alewives within the Lake Michigan ecosystem, our results will need to be incorporated into future bioenergetics modeling efforts. Bioenergetics modeling has already made an important contribution toward managing the salmon and trout populations in Lake Michigan, as management decisions to reduce Chinook salmon stocking rates have been partially based on results from bioenergetics models applied to salmon and trout populations to estimate annual consumption of alewives (Stewart et al. 1981; Stewart and Ibarra 1991; Hansen et al. 1993). More recently, a decision model, including a salmonine bioenergetics modeling component, has been developed to assist fishery managers in optimizing stocking rates of Chinook salmon (Szalai 2003). Most of these bioenergetics model applications to Lake Michigan salmonines have utilized the alewife energy density schedules developed by Stewart and Binkowski (1986). Our study has shown that use of the Stewart and Binkowski (1986) energy density schedules could result in underestimation of alewife consumption by 22.1% when bioenergetics modeling is applied to salmonine populations in Lake Michigan after 1994. More accurate estimation of alewife consumption by salmonines should lead to better decisions on salmon stocking rates. Therefore, we recommend that the energy density schedules presented in Table 1 be used when applying bioenergetics models to salmon and trout populations in Lake Michigan after 1994. Additionally, accuracy of annual estimates of consumption of invertebrates by the alewife population in Lake Michigan after 1994 would be improved by using the energy density schedules in Table 1 rather than the schedules presented in Stewart and Binkowski (1986). Hewett and Stewart (1989) have used the alewife bioenergetics model developed by Stewart and Binkowski (1986) to relate the degree of zooplanktivory by the alewife population to zooplankton abundance in Lake Michigan. Finally, we conclude that identifying the effects of an aquatic invader on the fish community is best facilitated by the availability of long-term observations on the various components of the food web. We relied on long-term time series for alewife abundance, alewife condition, and abundance of *Diporeia* in Lake Michigan to examine the effect of the dreissenid mussel invasion on alewife energy dynamics. Even though the objective of the study was focused on quantifying the effects of the dreissenid mussel invasion on alewife energy density, availability of data from the GLSC long-term survey of prey fish abundances in Lake Michigan allowed us to rule out the possibility that the decrease in energy density during the 1990s was due to an increase in alewife abundance. Further, the long-term series for alewife condition in Lake Michigan dropped abruptly in 1995 and condition remained at a relatively low level during 1995–2004, suggesting a dreissenid mussel ef-

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fect. Analogously, Madenjian et al. (2000*b*) relied on long-term time series for abundances of age-0 white bass and white perch, for abundances of adult white perch and white bass, and for phosphorus loading to Lake Erie to show that the reduction in white bass recruitment in Lake Erie was most likely due to the white perch invasion. Because the rate of invasions of freshwater fishes and invertebrates into aquatic ecosystems has increased in many areas around the world over the past three decades (Mills et al. 1993; Rahel 2000; Kolar and Lodge 2002), maintaining the long-term surveys of biota becomes even more critical in understanding and managing important aquatic ecosystems.

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Empirical analysis and transboundary management for Georges Bank multispecies fishery

Mark Lucas Soboil and Jon G. Sutinen

Abstract: This paper reports the results of a bioeconomic evaluation of alternative management strategies for the Georges Bank transboundary multispecies fishery. Because the distribution of the principal groundfish resources on Georges Bank involves substantial movement and migration across the US–Canada boundary, the harvest by one country affects the benefits to the other country. An empirically based model of the transboundary multispecies fishery was built to simulate alternative management strategies imposed by each country. The simulations were used to help determine whether the status quo management is superior to any other strategy and, if not, what other strategies are better in terms of economic performance. Our aim is to determine whether there are combinations of US and Canadian harvest policies that would make both countries better off and whether a "win–win" strategy exists in the fishery. The results suggest that there are win–win strategies in terms of economic benefits, but such strategies may not be legally feasible under current fisheries law.

Résumé : On trouvera ici les résultats d'une évaluation bioéconomique de stratégies de gestion de rechange pour la pêche commerciale transfrontalière et multispécifique du banc Georges. Puisque la répartition des ressources principales de poissons de fond sur le banc Georges implique d'importants déplacements et migrations de part et d'autre de la frontière É.-U. et Canada, la récolte dans un pays affecte les bénéfices du pays voisin. Nous avons élaboré un modèle à base empirique de cette pêche transfrontalière et multispécifique afin de simuler les stratégies de gestion de rechange imposées par chaque pays. Les simulations ont servi à déterminer si la gestion actuelle est supérieure à toute autre stratégie et, dans le cas contraire, quelles stratégies de rechange offrent la meilleure performance économique. Notre objectif est de déterminer s'il existe des combinaisons de politiques de récolte américaines et canadiennes qui favoriseraient les deux pays et de voir s'il existe une stratégie « gagnant–gagnant » dans cette pêche commerciale. Les résultats indiquent qu'il y a des stratégies de type gagnant–gagnant en ce qui a trait aux bénéfices économiques, mais que ces stratégies peuvent ne pas être légalement applicables étant donné la législation des pêches actuelle.

[Traduit par la Rédaction]

Introduction

This paper reports the results of a bioeconomic evaluation of alternative management strategies for Georges Bank transboundary multispecies fishery. Our aim is to determine whether there are combinations of US and Canadian harvest policies that would make both countries better off, i.e., whether a "win–win" strategy exists in the fishery.

Georges Bank in the Gulf of Maine is considered to be one of the most productive ocean areas in the world. Because it is shared between Canada and the US, the spatial distribution, spawning, and migration patterns of the principal groundfish resources create significant transboundary management concerns. Since extending fisheries jurisdiction and settling their boundary dispute, Canada and the US have taken different approaches to managing their groundfish fisheries in the region. The two countries' management practices have evolved differently in part because of variations in the structure and philosophies of the industry and administrative bodies.

Although both countries have implemented policies to manage these aquatic resources, historically neither had adopted policies that explicitly account for their transboundary nature. Before the 2004 US/Canada Resource Sharing Understanding (explained below) between the two countries, each country independently set their own harvest rates. Now that Canada and the US are coordinating their policies to some extent, potential conservation and management alternatives

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need to be examined to optimally manage the transboundary stocks.

We develop and apply a dynamic, bioeconomic simulation model to evaluate the consequences of alternative management strategies for Georges Bank groundfish fishery. The model incorporates both the biological and economic characteristics of the fishery. The biological component of the model describes the population and spatial dynamics of the principal groundfish stocks. The economic component describes the production technology and harvesting strategy of each nation and includes the harvest strategy for parts of the US otter trawl fleet, as well as the Canadian longline and otter trawl fleets. The fleets are differentiated by cost and harvest efficiency.

The bioeconomic models were combined with the catch equations to define stock and harvest relationships for several vessel length classes. These relationships were used to simulate alternative management strategies and determine whether the status quo management is superior to any other strategy and, if not, what other strategies are better in terms of economic performance. For each management alternative, the model simulated the change in profits for both countries jointly, as well as each country individually over a 20-year period, 2001 through 2020.

Background

Georges Bank is situated at the western end of a chain of banks extending from the Grand Banks of Newfoundland to Nantucket Shoals off the US coast. Today, it is used to describe the shallower part of Northwest Atlantic Fisheries Organization (NAFO) management area 5Z (Fig. 1). Since 1977, with the declaration of exclusive economic zones (EEZ) by coastal states, only Canada and the US have conducted fisheries for groundfish on the bank. Immediately before this, fisheries management on Georges Bank fell under the mandates of the International Commission for the Northwest Atlantic Fisheries (ICNAF) and was harvested by distant-water fleets from various nations.

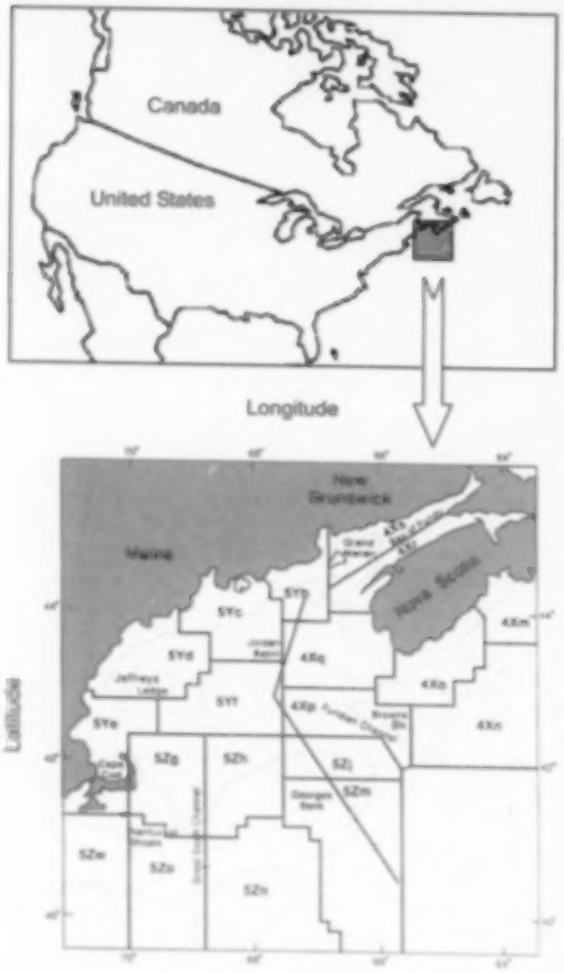
Multiple species characterize the groundfish fisheries on Georges Bank. Because the fishing gear cannot selectively harvest among individual species, there is joint production where vessels direct their effort at one species and also catch other groundfish species that inhabit the same areas (Kirkley and Strand 1988).

In 1986, the US developed a Multispecies Fisheries Management Plan that turned largely to input controls, namely area and season closures, mesh size, trip limits, etc. In addition, beginning in 1994, the US also implemented effort control measures to reduce fishing pressure on groundfish stocks. The key components of the effort control measures included a limited-entry program and days-at-sea (DAS) program that reduced the amount of time that a vessel owner can participate in the groundfish fishery. However, recent amendments (2004) to the DAS policy allows multispecies limited-access permit holders to permanently transfer DAS to other multispecies limited-access holders. The US groundfish fishery is harvested almost exclusively by mobile gear vessels that use bottom otter trawl gear.

By contrast, Canada has embraced output controls since the declaration of the EEZ, principally catch quotas for regulation and developed reporting and monitoring systems to support the quota system. Additional measures have included limited-entry licensing, fleet allocations, mesh size and hook size regulation, area and season closures, third-party 100% dockside monitoring to verify species and amounts landed, user pay at sea monitoring, minimum fish size through small fish protocol, mandatory reporting requirements, and mandatory landing requirements (no discards). Primarily inshore vessels conduct the Canadian fishery, with the fixed gear (longline and gillnet) having the larger cod share and bottom otter trawl gear having higher haddock quotas.

Recently, in 2004, Canada and the US reached an understanding through the US/Canada Resource Sharing Understanding (hereafter referred to as the Understanding) to share cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and yellowtail flounder (*Limanda ferruginea*) and limit the amount of fish that each country may catch. Other species landed by Canada and the US, but not part of the Understanding, include Acadian redfish (*Sebastes fasciatus*), white hake (*Urophycis tenuis*), pollock (*Pollachius virens*), win-

Fig. 1. Statistical unit areas on Georges Bank (inset shows location on east coast of Canada and the US).



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dowpane flounder (*Lophopsetta maculataa*), ocean pout (*Macrozoarces americanus*), and Atlantic halibut (*Hippoglossus hippoglossus*). Each country adopted specific restrictions and conditions to ensure that their respective fish limits were not exceeded. Clearly, the policies by Canada and the US must account for the impacts on each other's fisheries for the two countries to resolve their fisheries management concerns.

The economic analysis of transboundary fisheries has often drawn on the theory of noncooperative and cooperative games (Munro 1979, 1987). The game theoretic approaches have shown that transboundary resources that are jointly exploited in a noncooperative manner yield lower economic returns than those managed cooperatively. Alternatively, cooperative management, where the countries' management policies are complementary, can achieve superior outcomes. Armstrong and Flaaten (1991) and Aguero and Gonzalez (1996) applied Munro's model for the cooperative management of transboundary fisheries. Both studies estimated the extent to which that cooperative management is superior to noncooperative policies.

Game theoretic approaches, however, leave a few questions unanswered. To what extent are the groundfish harvests of one country reducing the benefits of the other country? To what extent, if at all, are the groundfish management measures of the two countries in conflict? How can the two countries' management measures be more complementary and support each other's management objectives? And what are the potential gains from cooperative management of the groundfish resources on Georges Bank?

To help answer some of these questions, we built on the conceptual framework developed by Soboil and Sutinen (2004) to examine transboundary fisheries and developed a bioeconomic model to assess the economic benefits from alternative management strategies for Georges Bank transboundary multispecies fishery. A dual-based revenue function was used to represent the economic characteristics of the US and Canadian multispecies fishery. The biological and spatial attributes of the fishery were incorporated to reflect the growth and seasonal migration of the groundfish stocks. After we empirically estimated all relationships, the model was used to simulate changes in the stock size, harvest rates, and economic profits over a 20-year period.

Materials and methods

Stock dynamics

The premise behind all the spatial models of the principal groundfish species in this paper is that there is seasonal movement of the stock between Canada and the US. If we postulate that in the spring a proportion of the US cod stock migrates into Canadian waters, we can express the Canadian spring cod stock size as

$$(1) \qquad x_{\text{Can,S}} = x_{\text{Can,F}} + \alpha x_{\text{US,F}} + F(x_{\text{Can,F}} + \alpha x_{\text{US,F}}) - h_{\text{Can,F}}$$

where $x_{\text{Can,S}}$ is the stock size in Canada during the spring, $x_{\text{Can,F}}$ is the stock size during the fall, $x_{\text{US,F}}$ is the US stock size during the fall, α is a migratory parameter that measures the proportion of the US stock that migrates into Canadian waters during the spring, and $h_{\text{Can,F}}$ is the Canadian harvest during the fall. The stock growth function, $F(x_{\text{Can,F}} + \alpha x_{\text{US,F}})$, takes the following form:

$$(2) \qquad F(x_t) = x_t + rx_t\left(1 - \frac{x_t}{K}\right)$$

where x_t is the stock size in year t, r is a growth parameter, and K is the carrying capacity. $F(x_t)$ is a function that represents the natural growth rate of the stock. The proportion of the cod stock remaining in the US in the spring would be

$$(3) \qquad x_{\text{US,S}} = (1 - \alpha)x_{\text{US,F}} + F((1 - \alpha)x_{\text{US,F}}) - h_{\text{US,F}}$$

where $h_{\text{US,F}}$ is the US fall harvest. On the same note, if a proportion of the Canadian stock migrates into US waters during the fall, we can express the US cod stock size as

$$(4) \qquad x_{\text{US,F}} = x_{\text{US,S}} + \beta x_{\text{Can,S}} + F(x_{\text{US,S}} + \beta x_{\text{Can,S}}) - h_{\text{US,S}}$$

where β is a migratory parameter that measures the proportion of the Canadian stock that migrates into US waters during the fall and $h_{\text{US,S}}$ is the US harvest during the spring. The proportion of the stock remaining in Canada during the fall would be

$$(5) \qquad x_{\text{Can,F}} = (1 - \beta)x_{\text{Can,S}} + F((1 - \beta)x_{\text{Can,S}}) - h_{\text{Can,S}}$$

where $h_{\text{Can,S}}$ is the harvest by Canada during the spring. Because the migratory patterns of the groundfish are different, we also constructed separate population dynamic models for haddock and yellowtail flounder, as well as a fourth model that was the combination of all other species harvested by the US and Canadian fleets. We expressed the seasonal migration of haddock as

$$(6) \qquad x_{\text{US,S}} = x_{\text{US,F}} + \beta x_{\text{Can,F}} + F(x_{\text{US,F}} + \beta x_{\text{Can,F}}) - h_{\text{US}}$$

$$(7) \qquad x_{\text{Can,S}} = (1 - \beta)x_{\text{Can,F}} + F((1 - \beta)x_{\text{Can,F}}) - h_{\text{Can}}$$

$$(8) \qquad x_{\text{Can,F}} = x_{\text{Can,S}} + \alpha x_{\text{US,S}} + F(x_{\text{Can,S}} + \alpha x_{\text{US,S}}) - h_{\text{Can,S}}$$

$$(9) \qquad x_{\text{US,F}} = (1 - \alpha)x_{\text{US,S}} + F((1 - \alpha)x_{\text{US,S}}) - h_{\text{US,S}}$$

The seasonal migration of yellowtail flounder was expressed as

$$(10) \qquad x_{\text{Can,S}} = x_{\text{Can,F}} + \alpha x_{\text{US,F}} + F(x_{\text{Can,F}} + \alpha x_{\text{US,F}}) - h_{\text{Can,F}}$$

$$(11) \qquad x_{\text{US,S}} = (1 - \alpha)x_{\text{US,F}} + F((1 - \alpha)x_{\text{US,F}}) - h_{\text{US,F}}$$

$$(12) \qquad x_{\text{Can,F}} = (1 - \beta)x_{\text{Can,S}} + F((1 - \beta)x_{\text{Can,S}}) - h_{\text{Can,S}}$$

$$(13) \qquad x_{\text{US,F}} = x_{\text{US,S}} + \beta x_{\text{Can,S}} + F(x_{\text{US,S}} + \beta x_{\text{Can,S}}) - h_{\text{US,S}}$$

For all other species, it was assumed that there was no seasonal migration. The fish stock in each country representing all other species can be expressed as

$$(14) \qquad x_{\text{Can},t+1} = x_{\text{Can},t} + F(x_{\text{Can},t}) - h_{\text{Can},t}$$

$$(15) \qquad x_{\text{US},t+1} = x_{\text{US},t} + F(x_{\text{US},t}) - h_{\text{US},t}$$

Economic dynamics

Similar to the methodology used by Kirkley and Strand (1988), we modeled the behavior of fishing vessels for the New England groundfish fishery by using a generalized Leontief revenue function. The generalized Leontief revenue function has since been applied to other studies to model multispecies fisheries, including the California multispecies

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trawl fishery (Squires and Kirkley 1991), the Papua New Guinea (PNG) longline tuna (*Thunnus albacares*) fishery (Campbell and Nicholl 1994), and others. The modified generalized Leontief revenue function that was used to model Georges Bank groundfish fishery can be expressed as

$$(16)\quad R(z, p, x) = \sum_i \sum_j \beta_{i,j}(p_i p_j x_i x_j)^{1/2} z + \sum_i \beta_i p_i z^2 x_i$$

where $R(z, p, x)$ is the revenue function, p_i is the output price of the ith species, x_i is the stock size for the ith species, and z is a composit input. We measured z by the product of length of vessel and days absent per vessel. z is more commonly measured as the product of gross registered tonnage and days absent per vessel. However, because gross registered tonnage and length of vessel can become interchangeable measures (Eric Thunberg, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA, ethunber@whsun1.wh.whoi.edu, personal communication), we retained use of length of vessel because of the type of cost data available for the analysis. Applying Hotelling's lemma, we obtain the input-compensated supply functions:

$$(17)\quad \frac{dR}{dp_i} = h_i = \beta_{i,i} z x_i + \beta_i z^2 x_i + \sum_j \beta_{i,j}\left(x_i x_j \frac{p_j}{p_i}\right)^{1/2} z$$

where the necessary symmetry condition requires that $\beta_{i,j} = \beta_{j,i}, i \neq j$.

The parameters for the input-compensated supply equations were estimated for selected vessel classes in the US otter trawl, as well as the Canadian longline and otter trawl fleets. The three length classes used in the US model were (*i*) length < 50 trawl, (*ii*) 50 ≤ length < 70 trawl, and (*iii*) length ≥ 70 trawl. The four length classes used in the Canadian model were (*i*) length < 45 longline, (*ii*) 45 ≤ length < 65 longline, (*iii*) length < 45 trawl, and (*iv*) 45 ≤ length < 65 trawl. Both US and Canadian length classes are expressed in feet (1 foot (ft) = 0.3048 m). The length classes were categorized to reflect different operational strategies and were consistent with Kirkley and Strand (1988), who observed that smaller fishing vessels tend to harvest inshore, and larger fishing vessels, offshore. The fleet categories were also consistent with the vessel size classes used by the National Marine Fisheries Service (NMFS) and Department of Fisheries and Ocean (DFO).

Each country's profit was determined by subtracting total costs from total revenue. The summation of the input-compensated supply functions multiplied by the ex-vessel demand in each vessel size class was used to estimate total revenue:

$$(18)\quad \mathrm{TR}_i = \sum p_i h_i$$

where TR_i is the total revenue for the ith vessel size class. The total costs in each class were estimated from the summation of variable and overhead costs, as well as salaries and wages. Variable costs can be expressed as

$$(19)\quad \text{Variable costs} = \text{cost} \cdot \text{day}^{-1} \times \text{DAS}$$

where DAS are the mean annual days-at-sea used by each vessel size class. In both the US and Canadian fisheries, wages have traditionally operated on the "lay" system, which divides the total revenue from each trip among crew, captain, and owner according to preset percentages. For the US and Canadian groundfish fishery, 60% of net revenues are divided between captain and crew after 40% goes to the boat (Eric Thunberg, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA, ethunber@whsun1.wh.whoi.edu, personal communication). Variable costs are the responsibility of the crew and are subtracted after the total revenue has been divided. The crew share formula can be expressed as

$$(20)\quad \text{Wages} = 0.60 \times \mathrm{TR}_i - \text{variable costs}$$

From eqs. 19 and 20, the total costs in each vessel class can be expressed as

$$(21)\quad \mathrm{TC}_i = 0.60 \times \mathrm{TR}_i + \text{overhead costs}$$

where TC_i is the total cost for the ith vessel size class. In each country, the fleets' total production depends on the total revenue and total costs for all vessel classes. From eqs. 18 and 21, the net discounted profits in each country can be expressed as

$$(22)\quad \pi_i = \frac{\sum \mathrm{TR}_i - \sum \mathrm{TC}_i}{(1 + r_i)^t}$$

where π_i is the net discounted profit and r_i is the social discount rate for country i.

Biological data

Canada and the US both undertake bottom trawl surveys to determine the abundance of groundfish stocks in statistical area 5Z. Between the two countries, three surveys are conducted annually for cod, haddock, and yellowtail flounder: the DFO survey in February, the NMFS spring survey in March, and the NMFS fall survey in October. Results obtained from the bottom trawl surveys were used to build the bioeconomic models used in our analysis. To help define the model for all other species, we used the sum of the landings and carrying capacities for witch flounder (*Glyptocephalus cynoglossus*), American plaice (*Hippoglossoides platessoides*), and winter flounder (*Pleuronectes americanus*).

The bottom trawl surveys helped determine the distribution of the principal groundfish stocks relative to the US–Canada maritime border and provided us with a "snapshot" of the stocks during the spring and fall time periods. A simple average of the NMFS spring and DFO surveys was used to characterize the stock distribution in the colder winter–spring period. An average of the NMFS fall surveys was used to depict the warmer summer–fall period. Survey biomass indices from 1991 through 2001 were used to estimate the stock distributions, with each survey given a 50% weighting. For the model that includes all other species, we assumed an equal distribution in both US and Canadian waters. The assumption that all other species were evenly distributed between Canada and the US may dampen the effects that they have in our simulations when measuring the net benefits for the alternative management strategies for cod, haddock, and yellowtail flounder. The results from the NMFS and DFO surveys are summarized, and we give the distribution of the principal groundfish stocks relative to the US–

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Table 1. Seasonal distribution of cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and yellowtail flounder (*Limanda ferruginea*) (1991–2001).

	Cod (%)	Haddock (%)	Yellowtail (%)	All other species (%)
Spring				
US	69	28	53	50
Canada	31	72	47	50
Fall				
US	69	28	53	50
Canada	31	72	47	50

Canada maritime border that was used in the analysis (Table 1).

Distribution patterns between the surveys reveal large-scale movements, especially for cod and haddock. Marked migrations were not noted for yellowtail flounder. These observations were consistent with previous studies that suggested cod and haddock migrate to shallower depths on the Bank for spawning during the colder winter–spring season and move to the deeper slopes during the warmer summer–fall season (Silverman 1983; Begg 1998; Van Eeckhaute et al. 1999).

Mean catch and abundance data, as well as the carrying capacity, for each of the principal groundfish species was also provided by NMFS and DFO and was used to estimate the parameters in the bioeconomic models. The gross annual groundfish landings, as well as spawning stock biomass (SSB), for the period 1982 through 2001 were used to estimate the growth parameters.

Economic data

The input-compensated supply equations were estimated using landings, price, effort, and vessel data for the years 1997 through 2001, maintained by National Oceanographic and Atmospheric Administration (NOAA) Fisheries and DFO. These data were provided at the fishing-trip level for each species grouping and vessel category. The spawning stock biomass used in this analysis was NMFS and DFO mean annual abundance data that were prorated month to month.

Cost data was obtained from surveys of fleet sectors involved in catching groundfish on Georges Bank. The University of Rhode Island surveyed the small trawl vessel fleet in 1996 (Lallemand et al. 1998) and the large trawl vessel fleet in 1997 (Lallemand et al. 1999). Various components of the Scotia–Fundy groundfish fishing fleet were surveyed for vessel performance in 1990–1991 (DFO 1993).

In this study we used the best available cost data. Despite the age of the data, the fleet structure has not changed dramatically. Secondly, there have been relatively low rates of inflation; over the last 5 years the producer price index (PPI) for agricultural goods in the US was approximately 1.5% (Bureau of Labor Statistics 2004). If costs have changed, the results would reflect an overall adjustment in the profits, but the relative impacts of the analysis would remain unchanged. Both surveys collected data on fishing business costs that included both variable and overhead costs. Variable costs included fuel, oil and lubrication, ice, food and water, bait (where applicable), offloading, consignment, supplies, and other trip costs. Overhead costs included association fees, permits, haul out, insurance, mooring, office expenses, professional fees, business taxes, vehicle, interest, repair and maintenance, and other overhead expenses. The prices used in the simulations were mean fixed prices for the years 1997 through 2001.

Table 2. Variable and overhead cost distribution in the US and Canada (US dollars).

	Variable cost per day	Overhead costs
US		
Trawl <50 ft	353.98	30 945.12
Trawl 50–70 ft	275.77	68 878.17
Trawl ≥70 ft	373.53	139 009.67
Canada		
4X GF Longline 35–44 ft	324.43	29 731.93
4X GF Longline 45–64 ft	669.11	69 394.42
4X GF Mobile 34–44 ft	205.44	38 570.09
4X GF Mobile 45–64 ft	409.98	70 878.97

Note: Source: US: Lallemand et al. (1998, 1999); Canada: DFO (1993). 1 foot (ft) = 0.3048 m.

A summary of the US and Canadian surveys is provided (Table 2). The data from all surveys were adjusted for inflation with the gross domestic product (GDP) implicit price deflator (Bureau of Economic Analysis 2004) and are in 2001 US dollars. In our calculation of net discounted profit, for the US we used a discount rate of $r = 0.07$, approved by the Office of Management and Budget (OMB 2004). Although we were unable to find an agreed social discount rate specific to the Canadian fishery, for purposes of tractability we also assumed a discount rate of $r = 0.07$.

Estimation of the model

The migratory parameters were estimated from the stock proportions found in area 5Z during the spring and fall bottom trawl surveys. They were calculated in the following manner: given that 44% of the 5Z cod stock is found in Canada during the spring and 31% during the fall, there is a net loss of 13% of the stock that migrates from Canadian waters into US waters between spring and fall. The proportion of the spring stock remaining in Canada during the fall would therefore be 0.70. The migratory parameters estimated for all stocks are provided (Tables 3 and 4).

Once all the migratory parameters were estimated, using ordinary least squares (OLS), we estimated the growth parameter, r, with SAS statistical software version 9.0 (SAS Institute Inc. 2000). The US and Canadian growth parameter estimates are also provided (Tables 3 and 4).

Next, we estimated the catch relationships for the bioeconomic model. Input-compensated supply equations were estimated by Zellner's seemingly unrelated regression technique with SAS version 9.0 (SAS Institute Inc. 2000). In cases where landings for the species groups were zero, they were assigned the arbitrarily low value of 0.01 pound. Implicit ex-vessel prices for the species groups were estimated by dividing the total revenue by the quantity landed. Land-

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Table 3. Canadian parameter estimates for the spring and fall.

Species	Migration parameters		Growth parameters		Statistical values	
	α	β	r	K	R^2	p value
Spring						
Cod (*Gadus morhua*)	0.200	0.38	0.060	173 424	0.660	<0.0001
Haddock (*Melanogrammus aeglefinus*)	0.270	0.16	0.064	295 354	0.390	0.0010
Yellowtail flounder (*Limanda ferruginea*)	0.033	0.05	0.170	49 392	0.560	<0.0001
All other species	0.000	0.00	–0.018	57 860	0.042	0.3875
Fall						
Cod (*Gadus morhua*)	0.200	0.38	0.520	108 390	0.880	<0.0001
Haddock (*Melanogrammus aeglefinus*)	0.270	0.16	0.140	350 420	0.610	<0.0001
Yellowtail flounder (*Limanda ferruginea*)	0.038	0.05	0.300	47 040	0.520	<0.0001
All other species	0.000	0.00	–0.02	57 860	0.024	0.4986

Table 4. US parameter estimates for the spring and fall.

Species	Migration parameters		Growth parameters		Statistical values	
	α	β	r	K	R^2	p value
Spring						
Cod (*Gadus morhua*)	0.200	0.38	0.18	260 136	0.91	<0.0001
Haddock (*Melanogrammus aeglefinus*)	0.270	0.16	0.17	205 246	0.84	<0.0001
Yellowtail flounder (*Limanda ferruginea*)	0.033	0.05	0.45	68 208	0.58	<0.0001
All other species	0.000	0.00	0.41	57 860	0.94	<0.0001
Fall						
Cod (*Gadus morhua*)	0.200	0.38	0.45	325 170	0.98	<0.0001
Haddock (*Melanogrammus aeglefinus*)	0.270	0.16	0.39	150 180	0.84	<0.0001
Yellowtail flounder (*Limanda ferruginea*)	0.033	0.05	0.54	70 560	0.81	<0.0001
All other species	0.000	0.00	0.70	57 860	0.96	<0.0001

ings were estimated at the trip level for each species grouping and vessel category (results from this analysis are shown in Tables 5 and 6).

Because landings were estimated at the trip level, we first determined the mean number of trips by each vessel class seasonally and then calculated the total seasonal harvest by each vessel class by multiplying the mean number of trips by the trip-level landings. The total annual catch harvested by all vessel categories was determined by summing the seasonal harvests.

To measure the total annual catch by each country, we estimated the proportion of the total annual catch that was harvested by all vessel classes. Once we had determined the ratio of mean annual catch to the vessel class landings, we multiplied this mean proportion to the total annual catch harvested by the vessel categories to estimate total overall landings. The mean number of trips and the proportion of total overall catch are provided (Tables 7 and 8, respectively).

Results

Simulations

The bioeconomic model integrates the stock and harvest relationships for all vessel length classes in both Canada and the US. It was used to simulate alternative management strategies and help determine whether the status quo management is superior to any other strategy and, if not, what other strategies are better in terms of economic performance. The simulations were used to search for a combination of US and Canadian harvest policies that would make both countries better off, a so-called win–win strategy.

For each management alternative, a numerical simulation was run that evaluated the change in spawning stock biomass (SSB), harvest, and profits for each country over a 20-year period, 2001 through 2020. The simulations were based on initial SSB taken from mean NMFS and DFO catch and abundance data and implemented in Microsoft Excel®. Mean seasonal price, effort, and vessel data were used to reflect the economic variables in the model.

The outcomes for alternative management strategies were examined by adjusting the harvest rate to simulate alternative policy changes that affect total allowable catch (TAC) settings and (or) DAS allocations (see eq. 17). For each alternative harvest rate, the annual catch in each country adjusted accordingly as the SSB approached its new bioeconomic equilibrium. The results of the alternative management strategies were presented graphically and used to help identify under what conditions win–win strategies could be achieved.

The interaction between the two countries' fisheries was captured in the model through the availability to harvest the same groundfish stocks. For example, those stocks with high migration rates (a large proportion of the stock migrates into the waters of the other) and tighter management in one country generally improved the harvest (and profits) in the other. Stocks with lower migration rates generally prevented the benefits from improved fisheries management to be shared with the other. Therefore, the extent to which harvest and

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Table 5. Canadian parameter estimates for the model with seasonal migration.

	Length < 45				45 ≤ length < 65			
	Cod	Haddock	Yellowtail flounder	Other species	Cod	Haddock	Yellowtail flounder	Other species
(*a*) Fall longline								
Effort	**0.0256**	**0.0037**	<0.0001	0.0043	**0.019**	0.0004	<0.0001	0.0061
	(0.0205)	**(0.0002)**		(0.3892)	**(0.0005)**	(0.6849)		(0.3916)
Effort squared	**<0.0001**	**<0.0001**	<0.0001	<0.0001	**<0.0001**	<0.0001	<0.0001	<0.0001
	0.0449	**(0.0221)**		(0.8175)	**(0.0106)**	(0.4292)		(0.5591)
Cod		–0.0023	<0.0001	–0.0024		0.0007	<0.0001	**–0.0085**
		(0.3650)		(0.6839)		(0.6691)		**(0.0669)**
Haddock	–0.0023		<0.0001	–0.0001	0.0007		<0.0001	0.0026
	(0.3650)			(0.9618)	(0.6691)			(0.2176)
Yellowtail flounder	<0.0001	<0.0001		<0.0001	<0.0001	<0.0001		<0.0001
Other species	–0.0024	–0.0001	<0.0001		**–0.0085**	0.0026	<0.0001	
	(0.6839)	(0.9618)			**(0.0669)**	(0.2176)		
(*b*) Fall trawl								
Effort	**0.0044**	**0.0024**	**0.0032**	**–0.0045**	–0.0007	**0.0021**	**0.0021**	–0.0002
	(0.0705)	**(<0.0001)**	**(0.0288)**	**(<0.0001)**	(0.6413)	**(<0.0001)**	**(0.0015)**	(0.7045)
Effort squared	**<0.0001**	**<0.0001**	<0.0001	**<0.0001**	**<0.0001**	**<0.0001**	<0.0001	<0.0001
	0.0031	**(<0.0001)**	(0.2292)	**(0.0015)**	**(0.0004)**	**(<0.0001)**	(0.2563)	(0.8566)
Cod		–0.0008	–0.0001	**0.0022**		**0.0009**	0.0001	**0.0018**
		(0.1872)	(0.4664)	**(0.0125)**		**(0.0139)**	(0.3306)	**(<0.0001)**
Haddock	–0.0008		<0.0001	**0.0017**	**0.0009**		<0.0001	**0.0004**
	(0.1872)		(0.8877)	**(<0.0001)**	**(0.0139)**		(0.3074)	**(0.0723)**
Yellowtail flounder	–0.0001	<0.0001		0.0001	0.0001	<0.0001		<0.0001
	(0.4664)	(0.8891)		(0.3697)	(0.3306)	(0.3074)		(0.2817)
Other species	**0.0022**	**0.0017**	0.0001		**0.0018**	**0.0004**	<0.0001	
	(0.0125)	**(<0.0001)**	(0.3697)		**(<0.0001)**	**(0.0723)**	(0.2817)	
(*c*) Spring longline								
Effort	**0.0283**	**0.0050**	**<0.0001**	**0.0016**	**0.0118**	**0.0050**	<0.0001	0.0009
	(<0.0001)	**(<0.0001)**	**(0.0008)**	**(0.0002**	**(0.0271)**	**(<0.0001)**		(0.8503)
Effort squared	**–0.0001**	<0.0001	<0.0001	**<0.0001**	**<0.0001**	**<0.0001**	<0.0001	**<0.0001**
	(<0.0001)	(0.1988)	(0.4467)	**(0.0006**	**(<0.0001)**	**(<0.0001)**		**(<0.0001)**
Cod		**–0.0053**	<0.0001	**0.0017**		**–0.0031**	<0.0001	0.0045
		(<0.0001)	(0.9410)	**(0.0137)**		**(0.0637)**		(0.2559)
Haddock	**–0.0053**		**<0.0001**	**–0.0005**	**–0.0031**		<0.0001	–0.0024
	(<0.0001)		**(0.0164)**	**(0.0287)**	**(0.0637)**			(0.1310)
Yellowtail flounder	<0.0001	<0.0001		<0.0001	(<0.0001	<0.0001		<0.0001
Other species	**0.0017**	**–0.0005**	<0.0001		0.0045	–0.0024	<0.0001	
	(0.0137)	**(0.0287)**	(0.6213)		(0.2559	(0.1310)		
(*d*) Spring trawl								
Effort	0.0017	**0.0013**	**0.0091**	**–0.0020**	**0.0045**	**0.0045**	**0.0051**	0.0002
	(0.2342)	**(<0.0001)**	**(<0.0001)**	**(0.0010)**	**(<0.0001)**	**(<0.0001)**	**(<0.0001)**	(0.7185)
Effort squared	<0.0001	**<0.0001**	**<0.0001**	<0.0001	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
	(0.6857)	**(<0.0001)**	**(<0.0001)**	(0.2502)	**(<0.0001)**	**(<0.0001)**	**(0.0778)**	**(<0.0001)**
Cod		**0.0012**	0.0001	–0.0008		–0.0004	<0.0001	**0.0012**
		(0.0138)	(0.1856)	(0.1894)		(0.2413)	(0.7809)	**(0.0019)**
Haddock	**0.0012**		<0.0001	**0.0026**	–0.0004		<0.0001	**–0.0004**
	(0.0138)		(0.3785)	**(<0.0001)**	(0.2413)		(0.2757)	**(0.0068)**
Yellowtail flounder	0.0001	<0.0001		–0.0001	<0.0001	<0.0001		<0.0001
	(0.1856)	(0.3785)		(0.1079)	(0.7809)	(0.2757)		(0.3141)
Other species	–0.0008	**0.0026**	–0.0001		**0.0012**	**–0.0004**	<0.0001	
	(0.1894)	**(<0.0001)**	(0.1079)		**(0.0019)**	**(0.0068)**	(0.3141)	

Note: *p* values are shown in parentheses below parameter estimates. Statistically significant values (*p* values < 0.1) are shown in bold.

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Table 6. US parameter estimates for the model with seasonal migration.

	Length < 50				50 ≤ length < 70				Length ≥ 70			
	Cod	Haddock	Yellowtail flounder	Other species	Cod	Haddock	Yellowtail flounder	Other species	Cod	Haddock	Yellowtail flounder	Other species
(a) Fall travel												
Effort	**0.0009** (<**0.0001**)	**0.0003** (<**0.0001**)	**0.0004** (<**0.0001**)	**0.0010** (<**0.0001**)	**0.0004** (<**0.0001**)	**0.0004** (<**0.0001**)	**0.0006** (<**0.0001**)	**0.0031** (<**0.0001**)	**0.0005** (<**0.0001**)	**0.0005** (<**0.0001**)	**0.0010** (<**0.0001**)	**0.0017**
Effort squared	**<0.0001** (<**0.0001**)	<0.0001 (0.8723)	<0.0001 (0.1376)	<0.0001 (0.3818)	<0.0001 (0.2697)	<0.0001 (0.6752)	**<0.0001** (0.0005)	**<0.0001** (<**0.0001**)	**<0.0001** (<**0.0001**)	**<0.0001** (<**0.0001**)	**<0.0001** (<**0.0001**)	**<0.0001** (<**0.0001**)
Cod	<0.0001 (0.4411)	**<0.0001** (0.0688)	**<0.0001** (0.0051)			**<0.0001** (0.0092)	**<0.0001** (0.0005)	**<0.0001** (0.0008)		**<0.0001** (0.0085)	**<0.0001** (0.0007)	**<0.0001** (0.0001)
Haddock	<0.0001 (0.4411)	**<0.0001** (0.0051)	**<0.0001** (0.0699)	**<0.0001** (0.0092)			**<0.0001** (0.0012)	**<0.0001** (<**0.0001**)	**<0.0001** (0.0085)		**<0.0001** (0.0085)	**<0.0001** (<**0.0001**)
Yellowtail flounder	**<0.0001** (0.0688)	**<0.0001** (0.0051)		**<0.0001** (0.0786)	**<0.0001** (0.0005)	**<0.0001** (0.0012)		**<0.0001** (0.0946)	**<0.0001** (0.0007)	**<0.0001** (0.0005)		**<0.0001** (<**0.0001**)
Other species	**<0.0001** (0.0051)	**<0.0001** (0.0699)	**<0.0001** (0.0786)		**<0.0001** (0.0008)	**<0.0001** (<**0.0001**)	**<0.0001** (0.0946)		**<0.0001** (<**0.0001**)	**<0.0001** (<**0.0001**)	**<0.0001** (<**0.0001**)	
(b) Spring travel												
Effort	**0.0002** (**0.0392**)	**<0.0001** (**0.0006**)	**0.0003** (**<0.0001**)	**0.0016** (**<0.0001**)	**0.0006** (**<0.0001**)	**0.0004** (**<0.0001**)	**0.0005** (**<0.0001**)	**0.0033** (**<0.0001**)	**0.0008** (**<0.0001**)	**0.0003** (**<0.0001**)	**0.0005** (**<0.0001**)	**0.0018** (**<0.0001**)
Effort squared	**<0.0001** (**0.0006**)	**<0.0001** (**0.0004**)	**<0.0001** (**<0.0001**)	<0.0001 (0.6666)	<0.0001 (0.7143)	**<0.0001** (**<0.0001**)	**<0.0001** (**<0.0001**)	**<0.0001** (**<0.0001**)	**<0.0001** (**<0.0001**)	**<0.0001** (0.0990)	**<0.0001** (**<0.0001**)	**<0.0001** (**<0.0001**)
Cod	<0.0001 (0.4800)	<0.0001 (0.3757)	<0.0001 (0.2086)			<0.0001 (0.6443)	**<0.0001** (0.0234)	**<0.0001** (**<0.0001**)		<0.0001 (0.1213)	**<0.0001** (0.0084)	**<0.0001** (**<0.0001**)
Haddock	<0.0001 (0.4800)		**<0.0001** (0.0219)	**<0.0001** (0.0568)	<0.0001 (0.6443)		**<0.0001** (0.0360)	**<0.0001** (**<0.0001**)	<0.0001 (0.1213)		**<0.0001** (0.0076)	**<0.0001** (**<0.0001**)
Yellowtail flounder	<0.0001 (0.3757)	**<0.0001** (0.0219)		<0.0001 (0.5229)	**<0.0001** (0.0234)	**<0.0001** (0.0360)		<0.0001 (0.4699)	**<0.0001** (0.0084)	**<0.0001** (0.0076)		**<0.0001** (**<0.0001**)
Other species	<0.0001 (0.2086)	**<0.0001** (0.0568)	<0.0001 (0.5229)		**<0.0001** (**<0.0001**)	**<0.0001** (**<0.0001**)	<0.0001 (0.4699)		**<0.0001** (**<0.0001**)	**<0.0001** (**<0.0001**)	**<0.0001** (**<0.0001**)	

Note: *p* values are shown in parentheses below parameter estimates. Statistically significant values (*p* values < 0.1) are shown in bold.

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Table 7. The mean number of trips in each vessel class.

Vessel categories	Cod		Haddock		Yellowtail		All other species	
	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
Longline								
Length < 45	165	26.2	165.2	26.2	0.2	0	128.8	17
45 ≤ length < 65	9.8	11.8	9.6	11.8	0	0	9.8	7.4
Trawl								
Length < 45	153.6	49	148.6	39.4	129.4	41.4	170.8	53.4
45 ≤ length < 65	134.6	61.2	135.8	58.6	75.8	34.8	131.6	57.8
Length < 50	23.2	69.2	31.6	2.2	43.2	23.6	73.8	26.8
50 ≤ length < 70	108.4	251.2	141.6	40.8	319.2	161.6	402	202.2
Length ≥ 70	322.6	802.4	586.4	179	641.6	260.8	727	407.8

Table 8. The proportion of the total annual catch in each country that was harvested by the vessel categories.

Species	US	Canada
Cod (*Gadus morhua*)	2.57	1.36
Haddock (*Melanogrammus aeglefinus*)	1.67	1.29
Yellowtail flounder (*Limanda ferruginea*)	1.13	1.06
All other species	0.8	0.23

profits changed in either country as a result of an adjustment in the management strategy depended on the rate of migration.

Given the significant rates of migration, the extent to which harvests and profits changed also depended on the harvest rate. A country with high harvest rates and tighter regulation would generally benefit both countries by increasing stock size, harvest, and overall profits. In countries where the harvest rate was already quite low, tighter regulation increased the overall stock size but also constrained catch and reduced profits. The next section describes in more detail the specific results from the numerical simulations.

Results of simulations

The results of the simulations are portrayed in a series of diagrams. In Fig. 2*a*, each line (one broken and the other solid) gives the locus of points for combinations of Canadian and US discounted profits over 20 years. The broken line shows combinations of estimated profits that result by changing Canadian policy and holding US policy constant. Point A represents status quo policy for both countries. Movement up and to the left from A along the broken line represents the consequences for profit combinations if Canada was to relax its regulations by increasing the harvest rate (relax TAC), holding US policy constant: Canadian profits increase and US profits decrease. Similarly, movement down and to the right from A along the broken line illustrates the consequences, in terms of profit combinations, if Canada was to reduce its TACs, holding US policy constant.

The solid line represents similar profit combinations for cases in which the US policy changes, holding Canadian policy constant at the status quo. An increase in the harvest rate in the US (relaxed DAS and (or) TAC policy), given the status quo Canadian policy, causes the US to become better off and Canada worse off. US profits also begin to decline as the stock become overfished. A reduction in the overall harvest rate in the US always makes Canada better off and the US worse off.

Each line demonstrates the economic consequences and conflicts created, when the countries set management policy independent of one another. In addition, the lines help define the conditions under which a win–win strategy could be achieved, i.e., both countries become better off (a Pareto improvement). To the right of the vertical dotted line, the US would become better off, and above the horizontal dotted line, Canada would become better off. In other words, the region above and to the right of point A represents potential win–win policy combinations, if they exist.

Next, we searched for alternative combinations of management policies that would make both countries better off (Fig. 2*b*). When we increased the harvest rates in Canada (relaxed TAC policies) and then kept them constant and proportionately relaxed US harvest rates, the first locus shifted out (shown in bold). Similarly, as we increased the harvest rates in the US (relaxed DAS and (or) TACs policies) and then kept them constant, together with proportional adjustments to the Canadian harvest rates, the second locus shifted up. The point at which the two loci meet, B, is the solution to the alternative management policy in which the total harvests in the US and Canada were 16% and 36% greater, respectively, than in the status quo policy (A).

The alternative policy B is also superior in terms of economic performance (12% and 7% increase in Canada and US profits, respectively). However, the adjustments in Canada and the US policies resulted in a lower SSB for all groundfish stocks. The change in SSB of cod is compared for the two different policies over the 20-year period (Figs. 3*a* and 3*b*). The sustainable SSB is smaller with alternative policy B than with the status quo policy A. As a result, the short-term gains from higher harvest rates (more relaxed management policy) may not satisfy each country's policy objectives and fisheries laws. For example, the fishing mortality that corresponds to the lower stock biomass in Fig. 3*b* falls close to the overfishing threshold ($F_{20\%}$) defined before Amendment 9 of the Magnuson–Stevens Act (MSA 1999). Therefore, this policy may be unfeasible and lead to an unacceptable risk of stock collapse.

We compared the change in nominal profits for policy A vs. policy B (Figs. 4*a* and 4*b*). We initially see that in the first few years there would be a considerable improvement in profits with the alternative policy. However, in later years, these gains are lost and eventually begin to approach those

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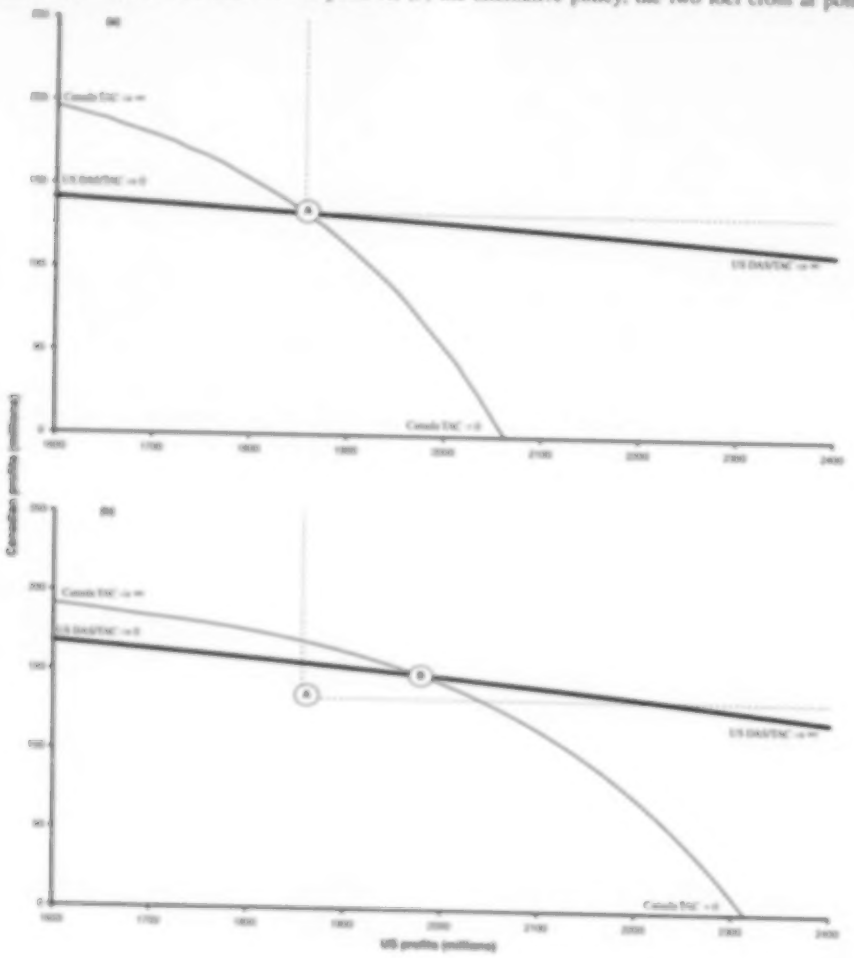
Fig. 2. Sum of profits for Canada and the US with changes to the total allowable catch (TAC) and (or) days at sea (DAS) allocation policies: (*a*) the status quo policy, the two loci cross at point A; (*b*) the alternative policy, the two loci cross at point B.



of the status quo policy. The profits from both policies begin to approach each other as a result of the tradeoff between higher harvest rates and smaller SSB and lower harvest rates and larger SSB. A smaller SSB ultimately lowers harvest and reduces profits, whereas a larger SSB ultimately increases harvest and profits improve. Also, just because the TAC may be relaxed to be a very large amount, the fleet does not necessarily catch it all, so there is still a large amount of sustainable catch that is possible.

To simulate the case of an alternative policy for individual stocks only, TACs were also adjusted and simulated over the 20-year period. Similar to the analysis used to search for superior management strategies, in the next set of simulations, we searched for conditions under which superior outcomes might be achieved with alternative harvest rates for individual stocks.

We present the results for which only the harvest rate for cod was adjusted, the harvest rate for all other stocks remained unchanged (Fig. 5). The point at which the two loci meet, C, was the win–win solution to the alternative policy. In alternative policy C, the US reduced the harvest rate of cod by 32% (tightened TAC policy settings) and Canada increased its harvest rate by 8% (relaxed TAC policy settings). The locus that reflects the change to the US harvest rate is backward bending because cod are considered to be overfished and increasing the US harvest rate would make both countries worse off. Alternative policy C improved the economic performance of the total groundfish fishery by 10.3% and 0.2% in Canada and the US, respectively. Although this is a win–win strategy, the economic gain for the US is negligible.

How could nominal profits in both countries be greater with the alternative policy C, while the harvest rate for cod in the US declined by as much as 32%? Cod is a stock of substantial transboundary migration, and harvest rates of cod are also significantly greater in the US than in Canada. With a high US harvest rate, tighter regulation provided an opportunity for the cod stock to rebuild. Together with the high

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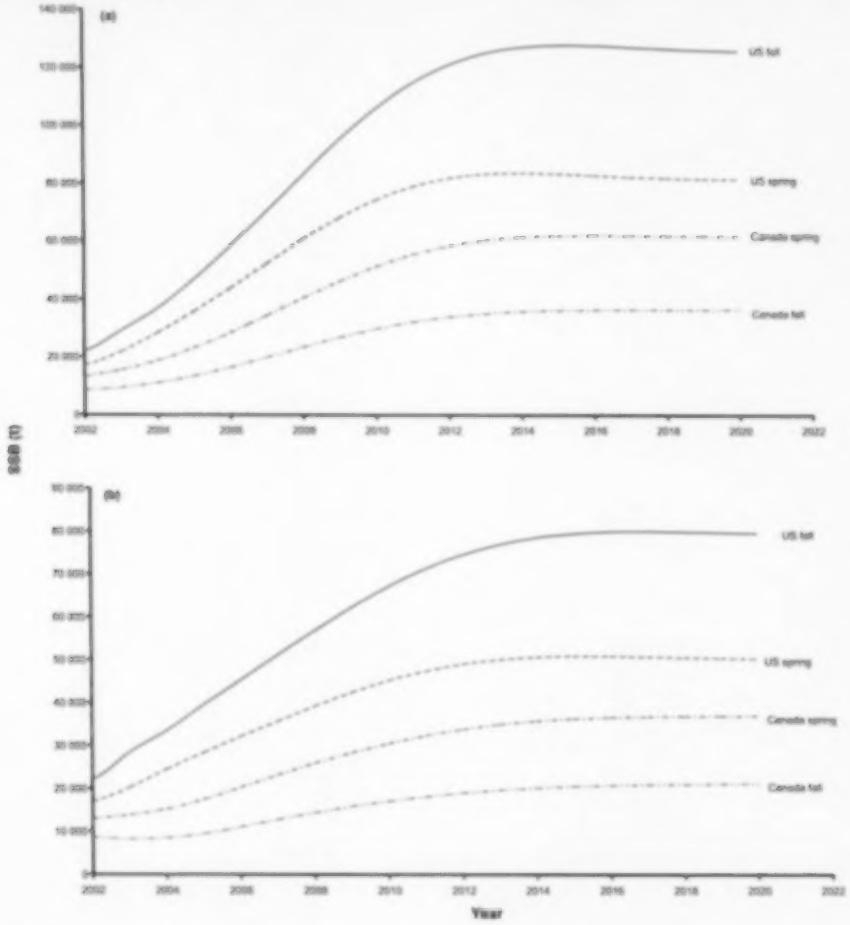
Fig. 3. The spawning stock biomass (SSB, tonnes (t)) of cod (*Gadus morhua*) in alternative seasons (*a*) under the status quo policy (A) and (*b*) under the alternative policy (B).



rates of migration, the larger SSB increased harvest, as well as profits, in both countries and both countries profited. Had a tighter regulation been imposed in Canada, the new harvest rate would have constrained catch and caused profits to decline in that country and only the US would have become better off.

Discussion

This paper presents an empirically based model of Georges Bank transboundary multispecies fishery and reports results of a bioeconomic simulation used to evaluate the consequences of alternative management strategies. Of special interest was whether we could find a combination of US and Canadian harvest policies that would make both countries better off, a win–win strategy. The results suggest that there may be economic benefits from alternative management strategies and there may be management measures that are more complementary that support each country's management objectives.

The problem of transboundary fisheries, which has often been cited in the literature, is that if neighbouring states do not cooperate they could act like competing harvesters. This has been illustrated by Levhari and Mirman (1980) and others. They showed that by applying the theory of noncooperative games, both countries could be driven to adopt strategies that would lead to the depletion of the resource. The issue is therefore well defined: whether or not the countries will cooperatively manage the resource.

Gulland (1980) pointed out that there are two levels of cooperative management. The first level of cooperation involves improved research to strengthen the management programs of each country. The second level involves coordinated joint management programs. In general, scientific information is freely available, and with the declaration of the EEZ, most countries regulate catch through either output controls or other regulatory measures. Canada and the US have already begun cooperatively managing the transboundary fishery on Georges Bank. This was realized with the Understanding in which each country agreed to share and limit their catch of cod, haddock, and yellowtail flounder. In the US, Amend-

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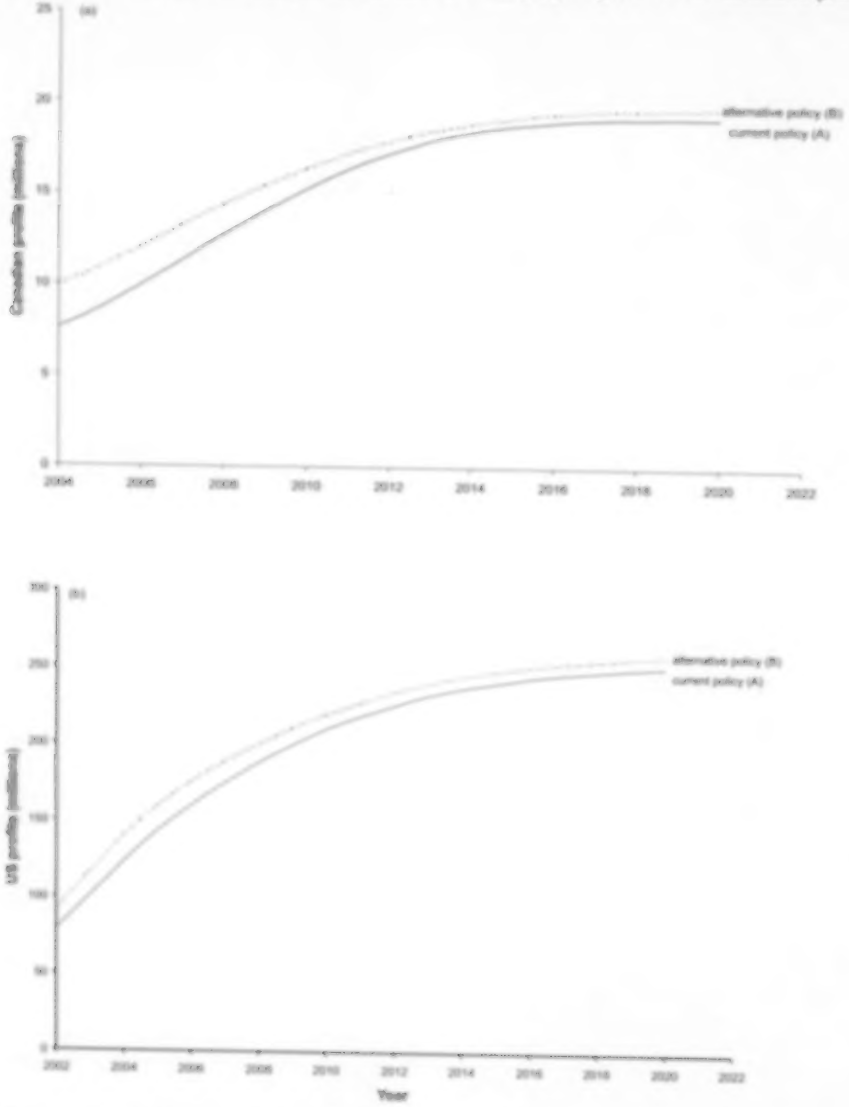
Fig. 4. Changes in annual profits in (*a*) Canada and (*b*) the US for the status quo policy (A) vs. the alternative policy (B).



ment 13 of the Multispecies Fishery Management Plan adopted specific restrictions and conditions to ensure that the US fish limits are not exceeded.

Often the question for countries that share fisheries is not whether they will cooperate but whether each country will benefit from more cooperatively managed resources. The benefits from cooperative management can only be realized if both countries realize benefits at least as great as they each would through noncooperation. For the Georges Bank fisheries, the opportunity or potential for significant gains from more cooperation (combination of US and Canadian harvest policies that would make both countries better off) depended on the initial conditions of the stock, i.e., the state of the fishery when the policy was invoked.

Haddock, for which both countries agree the stocks could sustain higher yields, were not negatively impacted by noncooperative management policies. Cod, however, were negatively impacted by noncooperative management policies, and both countries became better off by reducing harvest rates. These benefits from cooperative management were from stocks considered to be overfished.

Yellowtail flounder, which are considered to have low migration rates, did not benefit from more cooperative management policies. Munro (1987) also noted that some sedentary species, e.g., scallops, are not necessarily negatively impacted by noncooperative management policies. In both of these species where the rates of migration were low, the benefits from noncooperation were not inferior to the benefits from cooperation.

Any improvement from a change in policy depends critically on two factors: (*i*) migration rates and (*ii*) and harvest rates. Stocks with high migration rates that are confronted

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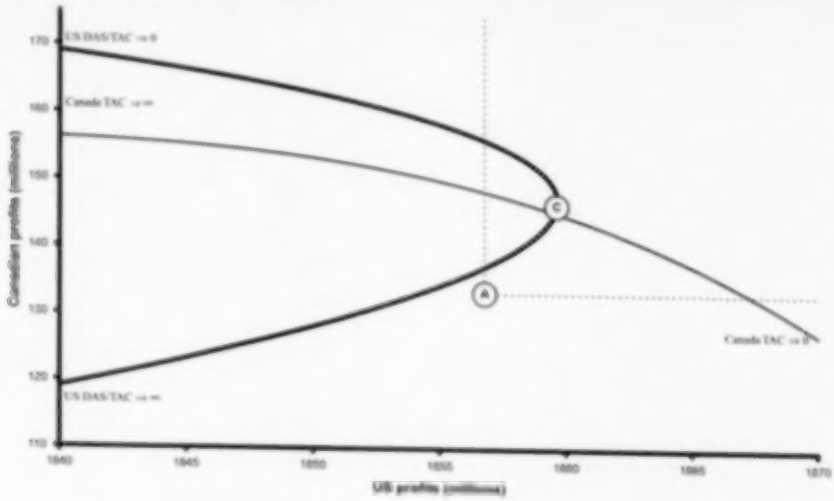
Fig. 5. Sum of profits for Canada and the US with a change in the total allowable catch (TAC) setting policy for cod (*Gadus morhua*) only. For the alternative policy, the two loci cross at point C.



with high harvest rates provide more opportunities for a combination of policies that can be complimentary and profitable for both countries. In such cases, improved management in one country will increase stock abundance to its neighbouring state. With large amounts of mixing, the reduction in catch in one country could favourably affect the availability to harvest in the other. Alternatively, when the harvest rates are low and the stock is abundant, there are fewer opportunities to find win–win strategies — both countries would become better off by increasing their individual catch. The bioeconomic simulations provide a useful tool to help understand the tradeoffs between low migration rates and high harvest rates.

Gulland (1980) noted that cooperative management contains three fundamental problems: (*i*) allocating catch shares among the countries; (*ii*) determining the optimal total catch rates over time; and (*iii*) implementing and enforcing the joint management program. This paper has attempted to address the first two problems. Munro (1987) claimed that after bargaining, it may be possible to find some reasonable and mutually acceptable formula for making allocations. However, even if an allocation proposal was agreed upon, the second problem, determining the optimal catch rates over time, is not as easy. Also, there are management conflicts such as different perceptions of the social discount rate, environmental concerns, production costs, biological bottom lines, and consumer tastes between countries. The conceptual framework from which the bioeconomic model was built seemed to capture most of the essential characteristics of the fishery in each country and provides a tool from which more informed allocation and policy (catch rate) decisions can be made.

A recent lawsuit won by the Conservation Law Foundation (CLF) charged that the NMFS violated federal law by risking further depletion of New England groundfish and resulted in additional DAS cutbacks. To make it viable for fishermen to remain in the fishery, there was a decision with Amendment 13 of the Multispecies Fishery Management Plan to allow transferable DAS, i.e., fishermen could pool their DAS. In theory, this policy would be similar to the outcome of transferable Individual Fishing Quotas (IFQs) in Canada. There would be an overall total quota for DAS and a price per quota similar to a shadow price or an opportunity cost not to harvest that would reflect the market for the transferable DAS.

Would the new transferable DAS policies affect the results of the empirical analysis? If the policy changes follow the theoretical change of implementing transferable quota, then in practice the results should differ. However, it would not be immediate for the policies to become effectively captured in the fundamental framework of the model. It may take considerable time before the order of magnitude of a change in the DAS or TAC will be observed. More important is that the underlying tradeoffs will not change, so the relative policy adjustments should continue to be measured effectively.

In our study, there seems to be two drivers that determine whether there are gains to be had from cooperatively managed fisheries: the migration rate and the harvest rate. This suggests that tuna and other highly migratory species that are shared by two or more countries will be negatively impacted by noncooperative management policies and the benefits from cooperation will be superior to the benefits from noncooperation. Hilborn and Sibert (1988) challenged the conventional view that skipjack and yellowfin tuna were highly migratory. They also suggested that the two drivers that would constrain the capacity of a coastal state to manage tuna fisheries would be the monthly emigration rate (the rate at which tuna move from one country's EEZ to the next) and the natural mortality rate. They argued that if the natural mortality is high relative to the emigration rate, then what goes on in one area will be of little consequence elsewhere.

However, in a more recent study, Sibert and Hampton (2003) noted several problems with the tagging data used in the Hilborn and Sibert study and estimated that the biological characteristics of skipjack and yellowfin tuna are such that their movements will carry a significant proportion of

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the population beyond most EEZs during their lifetime. Together with the Sibert and Hampton results, this suggests that international cooperation is necessary for effective conservation and management of highly migratory stocks. There are gains from cooperative management for shared stocks that are faced with high harvest rates and for which the migration rates are high. There are also potential economic benefits from alternative management strategies that are complementary and support each country's management objectives.

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The influence of fall-spawning coho salmon (*Oncorhynchus kisutch*) on growth and production of juvenile coho salmon rearing in beaver ponds on the Copper River Delta, Alaska

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Abstract: This study examined the influence of fall-spawning coho salmon (*Oncorhynchus kisutch*) on the density, growth rate, body condition, and survival to outmigration of juvenile coho salmon on the Copper River Delta, Alaska, USA. During the fall of 1999 and 2000, fish rearing in beaver ponds that received spawning salmon were compared with fish from ponds that did not receive spawners and also with fish from ponds that were artificially enriched with salmon carcasses and eggs. The response to spawning salmon was variable. In some ponds, fall-spawning salmon increased growth rates and improved the condition of juvenile coho salmon. The enrichment with salmon carcasses and eggs significantly increased growth rates of fish in nonspawning ponds. However, there was little evidence that the short-term growth benefits observed in the fall led to greater overwinter growth or survival to outmigration when compared with fish from the nonspawning ponds. One potential reason for this result may be that nutrients from spawning salmon are widely distributed across the delta because of hydrologic connectivity and hyporheic flows. The relationship among spawning salmon, overwinter growth, and smolt production on the Copper River Delta does not appear to be limited entirely to a simple positive feedback loop.

Résumé : Notre étude examine l'influence de la présence des saumons coho (*Oncorhynchus kisutch*) à reproduction automnale sur la densité, le taux de croissance, la condition corporelle et la survie des jeunes saumons coho jusqu'à l'émigration du printemps dans le delta du fleuve Copper, Alaska, É.-U. À l'automne 1999 et 2000, nous avons comparé les poissons élevés dans des étangs de castors qui reçoivent des saumons en fraye à des poissons provenant d'étangs qui ne reçoivent pas de reproducteurs et enfin à des poissons provenant d'étangs qui ont été artificiellement enrichis de carcasses et d'oeufs de saumons. La réaction à la présence de saumons reproducteurs est variable. Dans certains étangs, les saumons à reproduction automnale augmentent le taux de croissance et améliorent la condition des jeunes saumons coho. L'enrichissement par l'addition de carcasses et d'oeufs de saumons augmente significativement le taux de croissance des poissons dans les étangs qui ne contiennent pas de reproducteurs. Cependant, il y a peu d'indications que les bénéfices de croissance à court terme observés à l'automne entraînent une meilleure croissance durant l'hiver ou une plus grande survie jusqu'à l'émigration, par comparaison avec les poissons provenant des étangs qui ne reçoivent pas de reproducteurs. Une explication potentielle de ce résultat est que les nutriments provenant des saumons reproducteurs sont peut-être largement répartis dans tout le delta à cause de la connectivité hydrologique et des flux hyporhéiques. La relation entre les saumons reproducteurs, la croissance au cours de l'hiver et la production de saumoneaux dans le delta du fleuve Copper ne semble pas se limiter seulement à une simple boucle de rétroaction positive.

[Traduit par la Rédaction]

Introduction

The spawning and death of semelparous anadromous Pacific salmon (*Oncorhynchus* spp.) is recognized as an integral ecological process in freshwater ecosystems throughout the North Pacific Rim. Studies have revealed that this process influences primary productivity of streams (Richey et al. 1975; Wipfli et al. 1998) and the population dynamics

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and growth of secondary consumers (Wipfli et al. 1999), including juvenile salmonids (Eastman 1996; Bilby et al. 1998; Wipfli et al. 2003). Although studies have focused on the individual components involved in these processes, there is still much to be learned about the ecological relationships and consequences of spawning salmon (Gende et al. 2002).

The transport and delivery of marine-derived nutrients into streams by spawning salmon may be responsible, in part, for the high productivity of coastal Alaskan systems, especially in light of their oligotrophic nature (Mathisen et al. 1988; Kyle et al. 1997). The annual subsidy of nutrients from returning anadromous salmonids may induce a positive feedback loop where increases in productivity of multiple trophic levels lead to increased production of juvenile salmonids in streams (Michael 1995; Schmidt et al. 1998; Wipfli et al. 1998). This potentially results in larger numbers of adults returning to spawn, thus continuing the cycle.

A critical element of this positive feedback hypothesis is that juvenile salmonids experience heightened growth rates and greater survival to smolt outmigration because of energy acquired from eggs and carcasses. Growth and size have important implications in the overwinter survival of stream-rearing juveniles (Smith and Griffith 1994; Quinn and Peterson 1996) and in the ocean survival of smolts (Hager and Noble 1976; Bilton et al. 1982; Holtby et al. 1990).

Spawning salmon can directly and indirectly impact food availability and growth rates of juvenile, stream-rearing salmonids (Bilby et al. 1996, 1998; Eastman 1996). Carcasses and eggs from spawning salmon supply food and salmon-derived nutrients to freshwater ecosystems, and these nutrients are incorporated into freshwater food webs, including stream-rearing juvenile salmonids (Kline et al. 1993; Piorkowski 1995; Bilby et al. 1996). Fish can feed directly on carcasses and eggs (Bilby et al. 1998). Nutrients from carcasses can also be obtained by fish through the consumption of macroinvertebrates that feed directly on carcasses and on fungi and bacteria that colonize decaying carcasses (Wipfli et al. 1999). Spawning salmon can also increase invertebrate prey availability by their disturbance of streambed substrates that can dislodge benthic organisms (Peterson and Foote 2000).

Salmon eggs can make up a large portion of the diet of juvenile anadromous salmonids and resident trout during spawning (Eastman 1996; Bilby et al. 1998). Eggs are a high calorie food item (Bilby et al. 1998; Foote and Brown 1998), so their consumption can have short-term as well as long-term benefits. Spawning by coho salmon (*Oncorhynchus kisutch*) often occurs in the late fall or early winter, when metabolic rates may be depressed because of low water temperatures. A high quality food such as eggs supplies more energy per unit ingested, and some of the energy ingested above that required for maintenance can be stored (Weatherley 1972). The presence of an abundant, high quality food item, coupled with low water temperatures, may lead to relatively efficient growth (Brett 1971). The excess energy can be stored as lipid reserves that can be utilized when food availability decreases in the winter (Weatherley 1972).

The pristine streams of the Copper River Delta provide an excellent opportunity to examine the relationship between fall-spawning coho salmon and juvenile coho salmon. Most streams on the Copper River Delta have large runs of coho salmon from September through November. Beaver ponds dominate stream habitats on the Copper River Delta and generally have sufficient depth and cover to provide excellent rearing and overwinter habitat for juvenile coho salmon (Nickelson et al. 1992; Cunjak 1996). Beaver ponds also act as sinks that trap sediments, nutrients, and organic material, including salmon carcasses, which should be important to aquatic productivity (Cederholm et al. 1989; Wipfli et al. 1999). Beaver ponds downstream of spawning habitats may be hotspots of juvenile coho salmon productivity because spawning salmon and carcasses could stimulate food webs available to fish rearing in these ponds.

The purpose of this study was to examine the influence of fall-spawning coho salmon on the growth rate, density, and smolt production of juvenile coho salmon rearing in beaver pond habitats of the Copper River Delta. Density, growth rate, and survival to outmigration of juvenile coho salmon rearing in ponds directly influenced by spawning salmon were compared with those rearing in ponds without influence from spawning salmon and also with those rearing in ponds that were artificially enriched with salmon carcasses and eggs. The study focused on four main questions. (*i*) Were growth rates and body condition of juvenile coho salmon increased during salmon spawning? (*ii*) Were densities and growth rates of juvenile coho in beaver ponds with access to spawning salmon greater than those without such access? (*iii*) Could growth rates of juvenile coho in ponds without access to spawning salmon be increased through experimental introduction of salmon carcasses and eggs? (*iv*) Were smolt growth and survival to outmigration related to the presence of spawning salmon, carcasses, and eggs? A better understanding of the relationship between spawning salmon and juvenile coho salmon productivity may be important in future management of local fisheries and provide valuable insight into the ecological processes associated with spawning salmon in natural systems.

Materials and methods

Study area

The study was conducted in 12 beaver ponds located in two stream systems on the Copper River Delta, Alaska (Fig. 1). Eleven of the study ponds were in the Mile 18 stream system (60°26′N, 145°20′W) and one pond was located in an adjacent system known as Goose Meadows (60°26′N, 145°19′W; Fig. 1). The Mile 18 stream system is a fourth-order coastal floodplain river with a catchment area of ~15 km^2 and 21 km of stream channels. Mean stream surface gradient is 1%. The area receives ~380 cm of rainfall annually. Approximately 75% of the juvenile-rearing habitat is beaver ponds. Mean annual discharge is estimated at 1.0 m^3·s^{-1} and wetted widths are ~9 m during mean summer flow. The substratum is composed of alluvial gravels and cobbles. The Goose Meadows system is similar in size and other physical stream system characteristics.

The physical characteristics of the study ponds, except for surface area, were generally similar (Table 1). Pond sizes ranged from 324 to 4300 m^2. Primary cover for fish was

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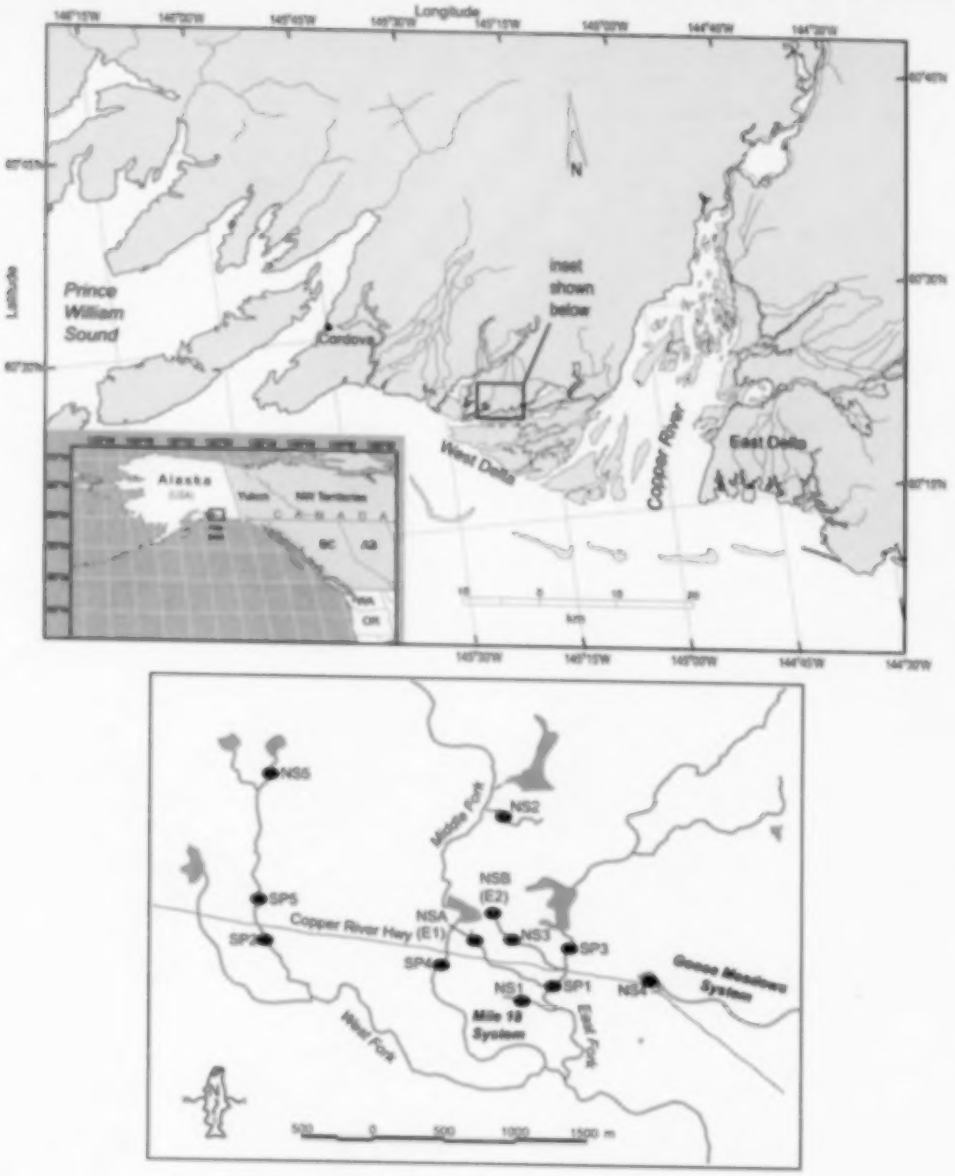
Fig. 1. Location of the study stream systems on the Copper River Delta, Alaska (USA.) and the study beaver ponds (lower inset map).



emergent aquatic vegetation and overhanging terrestrial vegetation. There were some pieces of small wood associated with the beaver dams, lodges, and caches in each pond, but large wood was not common.

The degree of influence by spawning salmon varied between beaver ponds used in the study (Table 1). Of the 12 ponds, five were directly downstream of spawning habitats and, therefore, influenced by spawning (SP1–SP5) while another five of the ponds (NS1–NS5) were located in either side channels or upstream of spawning areas (Fig. 1; Table 1). Two other ponds that were not influenced by spawning (NSA(E1) and NSB(E2)) were artificially enriched with salmon carcasses and eggs during the second year of the study. The mean number of fish observed during on-the-ground counts of spawning coho salmon in the stream directly above the influenced ponds was 197 and 179 fish in 1999 and 2000, respectively. The non-influenced ponds typically are not directly influenced by spawning salmon, but in some instances a few adult fish will get into these ponds. In 2000, six fish were seen spawning in and above pond NS4 (Table 1). Adult coho salmon entered these stream systems in early September, and spawning began in the last week of

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Table 1. Characteristics of the 12 beaver ponds and influence of spawning coho salmon (*Oncorhynchus kisutch*) during fall 1999 and 2000 on the Copper River Delta, Alaska.

Pond	Pond area (m^2)[a]	Max depth (m)	Water temperature during spawning (°C)[b]		Peak spawner count[c]	
			15 Sept. – 11 Oct.	11 Oct. – 8 Nov.	1999	2000
Ponds with no direct influence by spawning salmon, artificially enriched in 2000						
NSA(E1)	704	1.2	8.3	5.2	0	0
NSB(E2)	1779	1.1	7.8	4.8	0	0
Mean (SE)	1242 (538)	1.2 (0.1)	8.1 (0.3)	5.0 (0.2)	—	—
Ponds with direct influence by spawning salmon						
SP1	1588	1.7	6.6	3.6	234	194
SP2	1394	0.97	6.6	3.5	223	271
SP3	1011	—	6.2	4.4[d]	—	200
SP4	4298	1.5	7.8	4.9[d]	243	136
SP5	3147	—	7.1	4.6[d]	87	92
Mean (SE)	2288 (260)	1.4 (0.2)	6.9 (0.3)	4.2 (0.3)	197 (37)	179 (30)
Ponds with no direct influence by spawning salmon						
NS1	1432	1.7	7.1	3.7	—	0
NS2	1231	1.6	5.9	3.5	—	0
NS3	324	—	7.2	4.8[d]	—	0
NS4	9829	1.5	7.6	4.9[d]	—	6
NS5	692	1.8	6.7	4.9[d]	—	0
Mean (SE)	2702 (1793)	1.7 (0.1)	6.9 (0.3)	4.4 (0.3)	—	—

Note: Standard error (SE) is given after mean in parentheses.

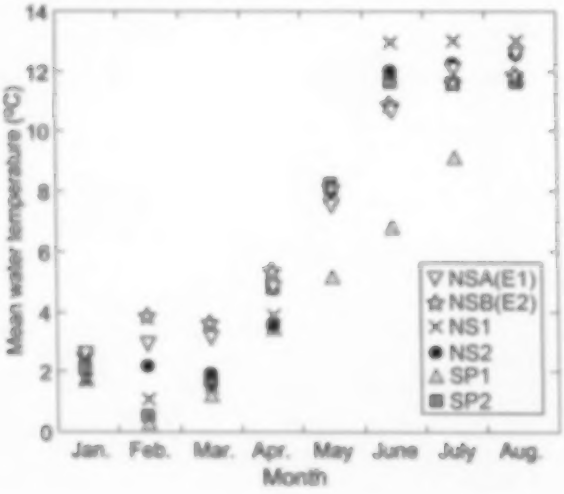
[a]Pond surface area measured using geographic information system (GIS) software.

[b]Mean water temperatures between sample dates during spawning in 2000 are shown. Temperatures were recorded hourly with Onset™ HOBO temperature data loggers placed midwater column at the deepest location in each pond.

[c]Peak count of spawners and carcasses within ponds and upstream of ponds is given. Approximate distance upstream that was included for each site was 100 m.

[d]Temperature recorders were removed during the week of 1 November rather than the week of 8 November.

Fig. 2. Mean water temperatures between sample dates over the summer and fall 2000 and over the winter and spring of 2001 in the beaver ponds with juvenile coho salmon (*Oncorhynchus kisutch*) tagged with passive integrated transponder (PIT) tags on the Copper River Delta, Alaska.



September. Peak counts of spawning salmon in the Mile 18 stream system were made in the third week of October in both years.

Water temperatures were monitored from July 2000 through August 2001 in six of the ponds (Fig. 2). In 2000, mean water temperatures between sample dates were recorded for all 12 ponds in time periods when salmon spawning occurred (Table 1).

Riparian habitats were similar around the ponds and dominated by Sitka alder (*Alnus sinuata*) and willow (*Salix* spp.). Sweetgale (*Myrica gale*), western hemlock (*Tsuga heterophylla*), and Sitka spruce (*Picea sitchensis*) were present to a much lesser degree. The aquatic plant communities were similar in all of the ponds. The dominant species included *Potamogeton* spp., burr reed (*Zostera* spp.), sedges (*Carex* spp.), and mare's tail (*Hippuris vulgaris*). Canopy cover was zero on all of the ponds. Pond substrates were predominantly composed of sand, silt, and organic material, but spawning-influenced ponds contained small pockets of gravels and cobbles where salmon spawned.

Age-0 and age-1 coho salmon were present in all the ponds. Threespine stickleback (*Gasterosteus aculeatus*), slimy sculpin (*Cottus cognatus*), coastrange sculpin (*Cottus aleuticus*), Dolly Varden (*Salvelinus malma*), and coastal cutthroat trout (*Oncorhynchus clarkii*) were also present in some ponds.

Density, growth rate, and body condition

In 1999, four ponds were sampled monthly beginning the week of 23 August and ending the week of 17 November. Two of these ponds (SP1 and SP2 in Fig. 1) were directly downstream of spawning habitats, and therefore juvenile coho salmon had access to salmon carcasses and eggs. The other

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Table 2. Schedule of introduction, volume of eggs, and number and biomass of carcasses added to the enriched ponds on the Copper River Delta, Alaska, in 2000.

	Litres of eggs (and biomass, kg)		No. of carcasses (and biomass, kg)	
Week of spawning run	NSA(E1)	NSB(E2)	NSA(E1)	NSB(E2)
1 Oct. – 7 Oct.	2 (2.6)	4 (5.2)	0	0
8 Oct. – 14 Oct.	3 (3.9)	6 (7.8)	4 (15.5)	11 (42.7)
15 Oct. – 21 Oct.	3 (3.9)	7 (9.1)	6 (23.3)	14 (54.4)
22 Oct. – 28 Oct.	2 (2.6)	4 (5.2)	8 (31.1)	20 (77.7)
29 Oct. – 4 Nov.	1 (1.3)	2 (2.6)	16 (62.2)	26 (101)
5 Nov. – 11 Nov.	1 (1.3)	2 (2.6)	13 (50.5)	25 (97.7)
12 Nov. – 18 Nov.	0	0	3 (11.7)	4 (15.5)
Total	12 (15.6)	25 (32.5)	50 (194)	100 (389)

Note: The volume of eggs was added throughout the entire pond at several times over the course of the week. Carcasses were introduced one at a time during the week and randomly distributed throughout the ponds.

two ponds were located in side-channels or in stream sections above available spawning habitats (ponds NSA(E1) and NSB(E2) in Fig. 1).

In 2000, six ponds were sampled monthly beginning the week of 5 July and ending the week of 8 November. Beginning in October 2000, ponds NSA(E1) and NSB(E2) were experimentally enriched with salmon carcasses and eggs. Ponds SP1 and SP2 were sampled again, and two ponds that were not influenced by spawning salmon were added to serve as controls to the enrichment (NS1 and NS2 on Fig. 1).

Juvenile coho salmon were captured each month with wire-mesh minnow traps baited with salmon roe. Traps were placed at approximately 10 m intervals in a grid-like fashion throughout each pond. Traps were set three times for 1.0–1.5 h to capture fish during each monthly sample. Traps were set once overnight in each pond during the months of October and November during both years, because water temperatures were below 6 °C and trap efficiency declined dramatically.

Growth rates of juvenile coho salmon were estimated by recapturing fish marked with passive integrated transponder (PIT) tags. During August and September 1999 and July, August, and September 2000, all individuals >60 mm from each pond were PIT-tagged, which gave them an individual identification number. Captured fish >60 mm were anesthetized with MS-222 (tricaine methanesulfate), measured to the nearest 1 mm fork length, and weighed wet to the nearest 0.1 g on an analytical balance and tagged. On these sampling dates, all fish <60 mm were measured and a subsample of 100 fish was weighed. All captured fish were used to estimate abundance and to formulate length–frequency distributions in the ponds. To identify PIT tags, all juvenile coho salmon >60 mm were scanned with an AVID™ PIT-tag receiver after the initial August 1999 and July 2000 trappings. The PIT-tag identification number was recorded along with the weight and length of the fish. After processing, all fish were placed into a recovery pen and released upon completion of the last trap set.

Percent weight gain per day was used as a measure of growth for individual recaptured PIT-tagged fish and was calculated with the following equation:

$$(1) \qquad G_t = [[(W_{t+1} - W_t)W_t^{-1}]D^{-1}] \times 100$$

where G_t is the relative growth rate expressed as percent initial weight gained per day over the growth period from capture at time t to recapture at time $t + 1$; W_t is the weight of an individual at time t, W_{t+1} is the weight of an individual at time of recapture, and D is the number of days occurring between time t and time $t + 1$. The relation between initial size and growth rates was examined (Lang 2003). There was no relation between size and growth rate, and we therefore did not consider size class in analyses for this study.

All juvenile coho salmon >60 mm captured from the ponds in September and November were used in a weight–length regression analysis to compare the change in body condition of fish between a before spawning and a during spawning sample. This was done with the fish captured from four ponds in 1999 and 12 ponds in 2000.

Six new ponds were sampled in 2000, three of which were naturally influenced by spawning (SP3–SP5 in Fig. 1). The other three ponds were not influenced by spawning salmon (NS3–NS5 in Fig. 1). Coho salmon were captured from the six new ponds using similar methods employed in the original ponds, except that fewer traps were used (~60% less effort) and a random subsample of 100 fish >60 mm was taken from the total number captured.

Experimental enrichment with salmon carcasses and eggs

Carcass and egg introductions attempted to mimic timing and magnitude of the natural spawning processes occurring in the Mile 18 stream system. During spawning in 1999 and 2000, field crews conducted weekly on-the-ground escapement surveys and recorded the number of spawners occurring within and directly upstream of ponds SP1 and SP2. The total number of spawning salmon within and above the ponds and the carcasses per area of pond were calculated at various times throughout the spawning run. Estimates from 1999 were used to calculate the expected number of carcasses needed for the introduction in 2000. Surveys conducted in 2000 were used to evaluate escapement numbers and timing of the run. Introduction of salmon eggs and carcasses to ponds E1 and E2 began in the first week of October 2000 (Table 2).

We collected 77 returning adult coho salmon from the Mile 18 stream system by hook-and-line. Fish were measured from mid-eye to tail fork to the nearest 1 cm and weighed to the nearest 0.1 kg. Egg skeins were removed

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Table 3. Estimated density (fish·m^{-2}) and standard error (SE) of estimate of juvenile coho salmon (*Oncorhynchus kisutch*) in six beaver ponds on the Copper River Delta, Alaska, during August and September 1999 and July, August, and September 2000.

	1999		2000		
Pond	August	September	July	August	September
Fish >60 mm					
Ponds with no direct influence by spawning salmon, artificially enriched in 2000					
NSA(E1)	0.28 (0.01)	0.35 (0.003)	No estimate[a]	0.16 (0.01)	0.22 (0.004)
NSB(E2)	0.05 (0.001)	0.14 (0.003)	0.15 (0.004)	0.19 (0.004)	0.28 (0.01)[b]
Mean	0.17 (0.12)	0.25 (0.11)	0.15	0.18 (0.02)	0.25 (0.03)
Ponds with direct influence by spawning salmon					
SP1	0.28 (0.01)	0.40 (0.04)[c]	No estimate[a]	0.14 (0.003)[b]	0.18 (0.05)[b]
SP2	0.29 (0.01)[b]	0.30 (0.01)	0.26 (0.02)	0.23 (0.01)[b]	0.29 (0.02)
Mean	0.29 (0.01)	0.35 (0.01)	0.26 (0.02)	0.19 (0.05)	0.23 (0.06)
Ponds with no direct influence by spawning salmon					
NS1	—	—	0.17 (0.001)	0.20 (0.01)	0.36 (0.01)
NS2	—	—	0.11 (0.01)	0.08 (0.001)[b]	0.10 (0.001)
Mean	—	—	0.14 (0.03)	0.14 (0.06)	0.23 (0.13)
Fish <60 mm					
Ponds with no direct influence by spawning salmon, artificially enriched in 2000					
NSA(E1)	0.18 (0.01)	0.20 (0.01)	2.89 (0.49)[c]	1.43 (0.04)[b]	1.59 (0.02)
NSB(E2)	0.07 (0.001)[b]	0.29 (0.01)	0.39 (0.14)	0.18 (0.01)[b]	0.29 (0.01)[b]
Mean	0.13 (0.06)	0.25 (0.05)	1.64 (1.25)	0.81 (0.63)	0.94 (0.65)
Ponds with direct influence by spawning salmon					
SP1	2.11 (2.60)[c]	1.39 (0.35)	No estimate[a]	0.52 (0.02)	0.88 (0.01)
SP2	0.53 (0.05)[c]	0.26 (0.01)	2.16 (0.32)	0.79 (0.02)[b]	0.85 (0.09)
Mean	1.32 (0.79)	0.83 (0.57)	2.16	0.66 (0.14)	0.87 (0.02)
Ponds with no direct influence by spawning salmon					
NS1	—	—	No estimate[a]	0.03 (0.01)	0.05 (0.01)
NS2	—	—	0.80 (0.07)[c]	0.26 (0.03)[c]	0.28 (0.002)
Mean	—	—	0.8	0.15 (0.12)	0.17 (0.12)

[a]No estimates were obtained as a result of poor depletion (equal or greater numbers captured on successive occasions as compared with the first).
[b]Estimates may be biased low (i.e., high proportion of total catch being captured on the first trap).
[c]Estimates may be biased high (i.e., poor depletion). (Based on χ^2 goodness-of-fit test where $p = 0.05$.)

from females if present and separated with a 2 cm mesh screen. Measured portions of eggs were placed in Ziploc® bags and stored in a refrigerator until introduction into the ponds. One female provided about 0.7 L (0.9 kg) of eggs after separation. Storage was typically 2–3 days.

The remaining whole fish were either frozen or placed directly into the ponds in a random fashion from a small boat. Frozen fish were thawed and placed randomly into the ponds at later dates (see Table 2). An additional 73 post-spawned carcasses were collected by hand from the Mile 18 stream and placed directly into the ponds or frozen for introduction at a later time (see Table 2).

Overwinter growth rate and survival to outmigration

A smolt weir was operated from 18 April to 2 July 2001 at the mouth of the Mile 18 stream system. The weir spanned the entire stream channel in a downstream-facing V formation. Migrating fish were funneled to the tip of the V by the weir itself (downstream migrants) or by a funnel supported by fence posts (upstream migrants). Fish were funneled into wooden holding boxes (0.6 m × 1.2 m), one on either side of the weir, catching upstream and downstream migrants. The boxes were checked daily during the period of operation. All outmigrating juvenile coho salmon were scanned with an AVID™ PIT-tag scanner. Tagged fish were anesthetized with MS-222, weighed to the nearest 0.1 g on an analytical balance, and fork length was measured. After recovery, the fish were released 50 m downstream of the weir. Juvenile coho salmon captured in the upstream box were scanned for PIT tags and then released 50 m upstream of the weir.

Overwinter growth was estimated based on the PIT-tagged fish recaptured at the weir. Growth rates (percent weight gain per day) were calculated using the time periods from capture in September, October, and November to recapture at outmigration. These time periods were used because they included the influence of spawning, if present, and overwinter and spring growth.

Survival to smolt outmigration was calculated as the percentage of tagged fish that were recaptured at the weir from the total number initially tagged in each pond during the previous summer and fall.

Statistical analyses

Abundance of juvenile coho salmon rearing in the ponds was estimated with the removal method when water temperatures were above 6 °C and the multiple trap-set schemes

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Table 4. Capture data for juvenile coho salmon (*Oncorhynchus kisutch*) >60 mm tagged with passive integrated transponder (PIT) tags in beaver ponds on the Copper River Delta, Alaska.

	July	August			September			October			November		
Pond	Total no. captured	Total no. captured	No. recaptured	% recaptured	Total no. captured	No. recaptured	% recaptured	Total no. captured	No. recaptured	% recaptured	Total no. captured	No. recaptured	% recaptured
1999													
NSA(E1)		151	NA	NA	220	116	76.8	185	106	41.6	109	58	22.7
NSB(E2)		84	NA	NA	138	63	75.1	158	51	32.1	104	23	14.5
SP1		360	NA	NA	421	97	24.3	41	10	2.5	42	13	3.3
SP2		337	NA	NA	374	191	56.7	76	19	5.1	47	4	1.1
2000													
NSA(E1)	72	101	45	62.5	168	71	51.4	32	12	5.5	137	15	6.9
NSB(E2)	231	320	143	61.9	457	289	70.8	118	36	6.3	344	79	13.7
SP1	151	226	22	14.6	261	35	10.4	47	13	2.3	160	14	2.5
SP2	279	293	122	43.7	326	173	38.4	19	8	1.3	30	6	1.0
NS1	207	255	105	50.7	399	182	50.3	420	230	63.5	358	78	21.5
NS2	122	101	86	70.5	116	99	72.3	36	10	6.5	60	7	4.5

Note: Total number captured is all coho salmon >60 mm captured during the particular sample month. Number recaptured is the number of fish with PIT tags that were captured during the sample month. Percent recaptured is the number of fish with PIT tags that in the sample month expressed as a percentage of all the PIT tags that were placed in the pond prior to the sample month. See text for definition of pond types. Because ponds were not sampled in July of 1999, there were no recaptured fish in August of 1999 (NA).

were incorporated (Zippin 1958; Bryant 2000). By October in both years, water temperatures had dropped below 6 °C, and minnow traps were set out once overnight. Thus, no depletion population estimates were computed after September. The computer software program MARK was used to obtain population estimates for juvenile coho salmon with the removal method (Zippin 1958; White and Burnham 1999). MARK performs a χ^2 goodness-of-fit test to check the assumption of equal probability of capture required in the removal model (White et al. 1982). Failure of the χ^2 goodness-of-fit test can result from having a high probability of capture on the first occasion relative to the other occasions, in which case the true abundance tends to be underestimated (White et al. 1982; Riley and Fausch 1992). A poor depletion (greater or equal numbers captured on successive occasions as compared with the first occasion) can also be responsible for failure of χ^2 goodness-of-fit tests. A poor depletion tends to overestimate true abundance (White et al. 1982).

Mean growth rates of recaptured PIT-tagged fish between monthly samples were calculated for each pond, resulting in three and four time periods in 1999 and 2000, respectively. Fish had to be captured in both the beginning and ending dates of a monthly time period to be included in the analysis of growth for that period. For example, to be included in the August–September estimate of growth, a PIT-tagged fish had to be captured in the August and in the September samples in a given pond. Few fish were recaptured in November that had also been captured in October; therefore, we did not use the October–November time period in our analysis. However, sufficient numbers of fish were recaptured in November that had been captured in September, so this time period was used to compare growth. Spawning and enrichment began in mid-September and at the start of October, so the time periods of September–October and September–November were considered time periods during spawning, while the ones before spawning included August–September 1999 and July–September and August–September 2000.

The response of growth rate to spawning and enrichment within individual ponds was compared with *t* tests. In this analysis, the mean growth rates of fish in the August–September time period were compared with growth during the September–October and September–November periods within each pond. Wilcoxon rank-sum tests were performed with the same data and were in agreement with the *t* test results. The results of the *t* test with unequal variances were reported if the Brown–Forsythe test for homogeneity in variances was significant ($p < 0.05$).

Weight–length regressions were used to compare body condition of juvenile coho salmon >60 mm between spawning periods in 2000 (Cone 1989). A test for significance between before spawning (September) and during spawning (November) samples within each pond was done with the multiple regression model:

$$(2) \quad \ln \text{weight} = \beta_0 + \beta_1(\ln \text{length}) + \beta_2(\text{sample time}) + \beta_3(\ln \text{length})(\text{sample time})$$

where β_0 is the intercept determined by the regression, β_1 is the slope of the regression, β_2 is a coefficient for the indicator of sample time (September vs. November), and β_3 is the

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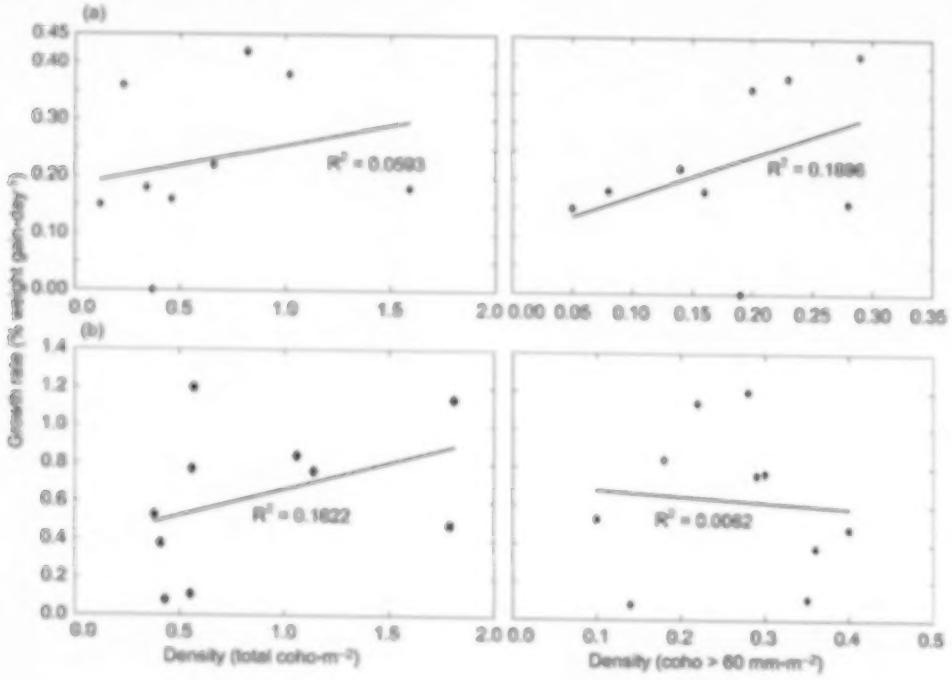
Fig. 3. Linear relationship between growth and density of passive integrated transponder (PIT)-tagged juvenile coho salmon (*Oncorhynchus kisutch*) trapped in beaver ponds on the Copper River Delta, Alaska. Densities at the beginning of the growth periods shown were used in the analysis, and total density was the combined density estimate of coho salmon >60 mm and <60 mm in length. (*a*) August–September; (*b*) September–October.



coefficient of the interaction term. If the slopes were not significantly different (test for $\beta_3 = 0$; $p > 0.05$), this variable was dropped from the model and the parallel lines model was used to test for the significant differences between samples (before vs. during) (Eastman 1996).

Results

Influence of spawning on density of salmon rearing in beaver ponds

In 1999, there were no significant differences in estimated density of fish (>60 mm) between the spawning and nonspawning ponds (Table 3; $p = 0.49$ and 0.53 for August and September estimates, respectively; *t* tests). There was high variation between the densities rearing in the two nonspawning ponds in both months (Table 3). In 2000, there were no significant differences in estimated fish densities (>60 mm) among the three pond types (Table 3; $p = 0.76$ and 0.98 for August and September estimates, respectively; analysis of variance (ANOVA) *F* tests). Again there was high variation between the densities of fish rearing in the nonspawning ponds (Table 3). Fish density (>60 mm) increased over time in most ponds during both years, but most increases were small and were likely the result of recruitment of fish from the 50 mm size class rather than immigration into ponds. Movement of tagged fish among ponds was minimal. Only 29 fish (0.6% of the total fish marked) were ever recaptured in ponds other than where they were marked. There were two exceptions to this low rate of immigration observed for fish >60 mm. In pond NS1, estimated density nearly doubled between August and September 2000. In pond NSB(E2), estimated density nearly tripled between the August and September 1999 samples (Table 3). The large increase in the total number of fish >60 mm captured during trapping (Table 4) provides additional evidence that fish moved into these ponds.

There was high variability in estimated densities within and among pond types for fish <60 mm (Table 3). In 1999, there were no significant differences between the pond types in either month ($p = 0.37$ and 0.49 (two-sided) for August and September, respectively; *t* tests). In 2000, there were no significant differences among the three pond types ($p = 0.51$ and 0.40 for August and September, respectively; ANOVA *F* tests). Although the variability within and between ponds was great, there was a general pattern of greater fish density (<60 mm) in the ponds adjacent to spawning habitats. In August and September, the estimated mean density of fish <60 mm in the ponds adjacent to spawning habitats was three to four times that in the nonspawning ponds (Table 3). The exception was in pond NSA(E1) where high densities of fish <60 mm were found during July, August, and September of 2000 (Table 3).

Influence of spawning on growth rate during spawning

We tagged 4609 juvenile coho salmon over 2 years: 1886 fish in 1999 and 2723 fish in 2000. The percentage of PIT-

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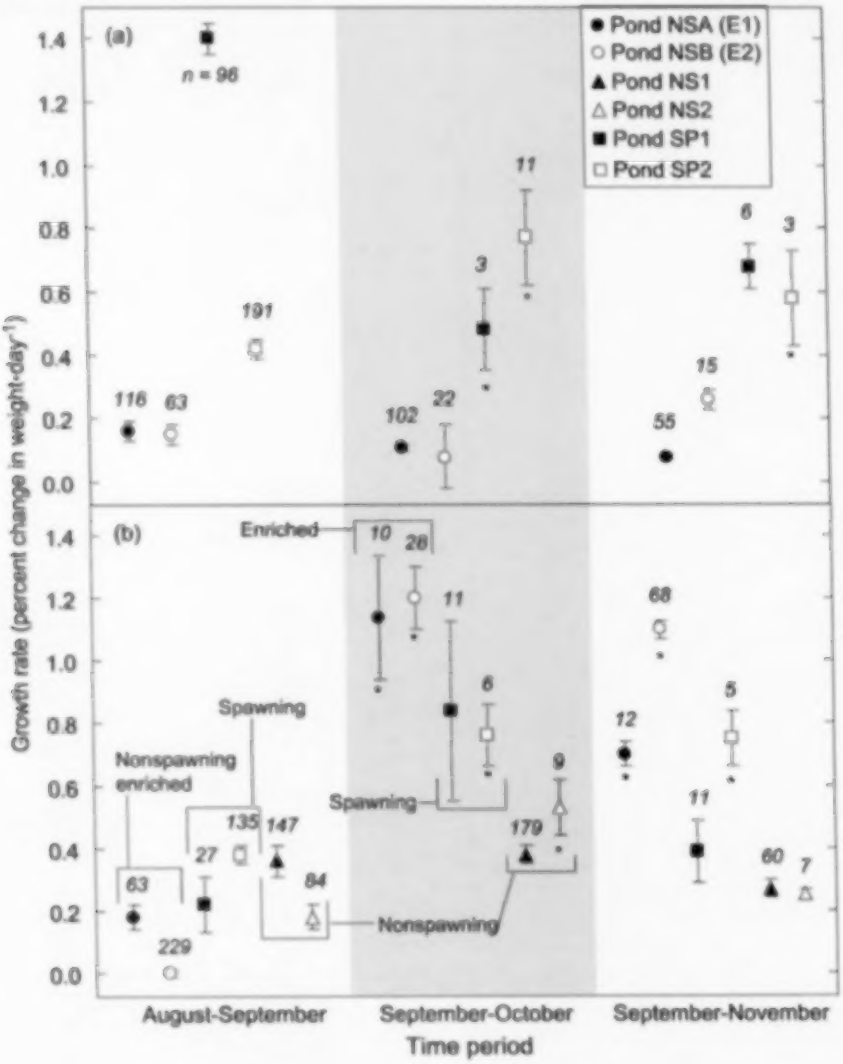
Fig. 4. Estimated mean growth rates (±1 standard error) of passive integrated transponder (PIT)-tagged juvenile coho salmon (*Oncorhynchus kisutch*) recaptured over the time periods before (August–September) and during (September–October, September–November) spawning in (*a*) 1999 and (*b*) 2000 on the Copper River Delta, Alaska. Numbers next to each frame indicate sample sizes for estimates. An asterisk (*) denotes a significant difference ($p < 0.05$) in growth of fish recaptured in a particular pond during spawning periods (September–October, September–November) as compared with those that were captured in the same pond before spawning (August–September).



tagged fish recaptured in the ponds during monthly sampling varied from 1.0% to 76.8% (Table 4). Recapture percentages tended to be highest in August and September and were lowest during spawning in October and November. Total number of fish >60 mm captured during the monthly samples generally decreased during spawning periods (Table 4).

There was no evidence of a density-dependent effect on growth rate in this study (Fig. 3). There was no significant relationship between total fish density or specific size class densities and growth rates during any of the time periods when both growth and density could be measured (August–September: total density, $p = 0.52$; density for fish > 60 mm, $p = 0.24$. September–October: total density, $p = 0.25$; density for fish > 60 mm, $p = 0.83$).

In 1999, growth rates of recaptured PIT-tagged fish were consistently greater in both the spawning ponds (SP1 and SP2) over all of the time periods (Fig. 4). There was no significant ($p > 0.05$) change in growth rate between time periods within either nonspawning pond (NSA and NSB, 1999). In the spawning ponds (SP1 and SP2), there were differences in growth rates between time periods but the patterns of growth were different (Fig. 4). In pond SP1, growth rates

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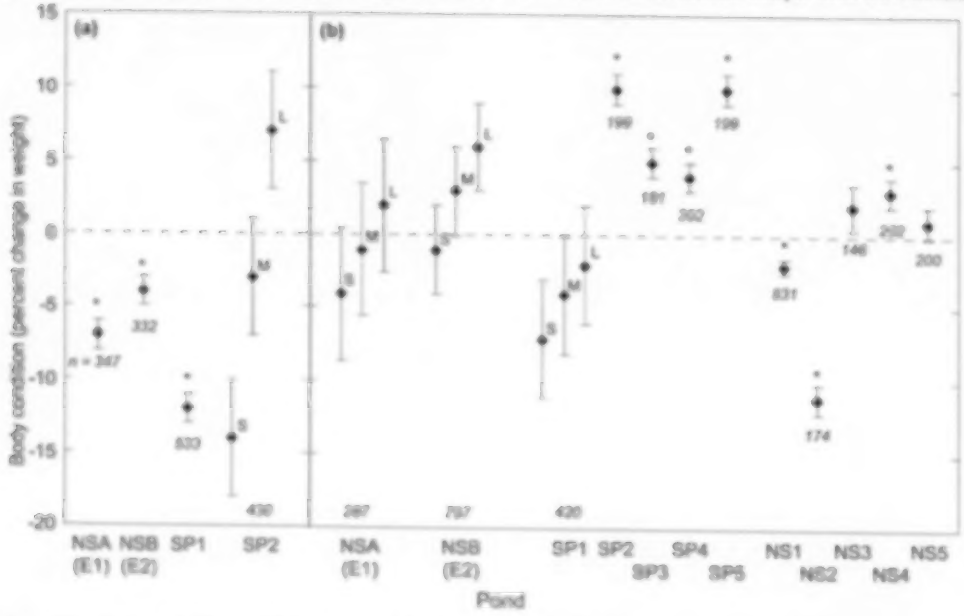
Fig. 5. The influence of spawning on body condition of juvenile coho salmon (*Oncorhynchus kisutch*) >60 mm captured in four beaver ponds in 1999 (*a*) and 12 beaver ponds in 2000 (*b*). The percent change in weight was predicted by regression models for fish of the same length sampled during spawning (November) as compared with before spawning (September). Negative values indicate a decrease in weight during spawning compared with before spawning. An asterisk (*) denotes that the regression was significant ($p < 0.001$). In ponds where interaction was significant (i.e., regression lines not parallel), three representative lengths (S = 60 mm, M = 80 mm, L = 100 mm) were used to get the corresponding percent change in weight. Numbers next to each frame indicate sample sizes for estimates.



decreased significantly ($p < 0.001$, two-sided t tests) during both spawning time periods relative to before spawning (Fig. 4). In pond SP2, growth rates increased in both time periods during spawning relative to before spawning. The estimated difference in mean growth rate for fish in this pond was significant ($p = 0.01$, two-sided t tests) between the August–September and the September–October time periods but not between the August–September and the September–November time periods ($p = 0.44$, two-sided t test).

In 2000, the highest mean growth rates for recaptured PIT-tagged fish were observed in the enriched ponds (NSA(E1) and NSB(E2)) over the spawning time periods, which corresponded with the addition of salmon eggs and carcasses. The nonspawning ponds (NS1, NS2) had the lowest growth rates during the spawning time periods, whereas the spawning-influenced ponds (SP1, SP2) exhibited an intermediate level of growth (Fig. 4). Growth rates significantly increased in ponds NSA(E1) and NSB(E2) ($p < 0.001$ in both ponds and time periods; t tests) during the egg and carcass enrichment relative to that before enrichment (Fig. 4).

Growth rates increased in the spawning-influenced ponds over the spawning time periods relative to that before spawning in 2000. However, the differences in growth rate between time periods were significant only in pond SP2 ($p = 0.01$ for both periods, two-sided t tests).

In pond NS1, growth rates did not differ significantly between any of the time periods, but in pond NS2 growth rates significantly increased during the September–October time period relative to the August–September time period ($p = 0.005$, two-sided t test).

Influence of spawning on body condition during spawning

In 1999, spawning did not improve the body condition of most juvenile coho salmon. In ponds NSA, NSB, and SP1, fish of the same length weighed significantly less ($p < 0.001$) during spawning as compared with fish sampled in these ponds before spawning (Fig. 5*a*). In pond SP2, there was a significant ($p < 0.05$) interaction between the length–weight relationships before and during spawning. This indicated that the response of fish body condition to spawning depended on fish size. Larger fish (~100 mm) weighed more during spawning than before spawning, but the medium (~80 mm) and small (~60 mm) fish weighed less during spawning than before (Fig. 5*a*).

In 2000, the body condition of juvenile coho salmon in the spawning ponds generally improved during the spawning period. In ponds SP2–SP5, fish of the same length were significantly ($p < 0.001$) heavier during spawning than before (Fig. 5*b*). The increase in mean weight for fish of the same length in these ponds ranged from 4.2% to 11.4%. In pond SP1, the response of body condition to spawning varied with fish size, but condition was always less during spawning regardless of fish size (Fig. 5*b*).

In the enriched ponds, the body condition of medium-sized fish in pond NSB(E2) and of larger fish in both ponds were improved by the presence of carcasses and eggs (Fig. 5*b*). Small fish in both ponds did not show an improvement in body condition during the enrichment.

The change in body condition of juvenile coho salmon in the nonspawning ponds (NS1–NS5) varied during the spawning period (Fig. 5*b*). In two of five ponds (NS1 and NS2),

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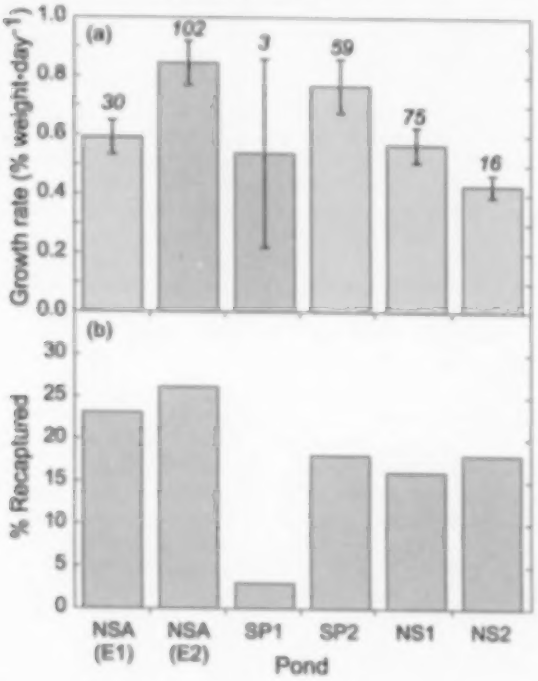
Fig. 6. Estimated mean (± standard error) growth rate (*a*) and survival to outmigration (*b*) of recaptured passive integrated transponder (PIT)-tagged juvenile coho salmon (*Oncorhynchus kisutch*) over the time period from the fall 2000 to smolt outmigration in the spring 2001 on the Copper River Delta, Alaska.



body condition decreased significantly ($p \leq 0.0001$) during spawning. The decrease in mean weight for fish of the same length was 2.1% (NS1) and 11.8% (NS2) (Fig. 5*b*). There was no major change in body condition associated with the spawning period in pond NS3 and NS5 (Fig. 5*b*). In pond NS4, the body condition of fish was significantly ($p < 0.0001$) improved during the spawning period.

Influence of spawning on overwinter growth rate and survival to outmigration

There was no significant difference in growth rate or survival over the winter between the ponds based on the recapture of PIT-tagged fish at the weir (Fig. 6; growth, $p = 0.22$; survival, $p = 0.23$; ANOVA F tests).

Discussion

The influence of natural spawning on growth rate and body condition of juvenile coho salmon was quite variable between years, ponds, and sizes of fish. There were no consistent patterns observed in these variables for spawning and nonspawning ponds. Although growth rates of fish in the spawning ponds were generally greater during the spawning period, small sample sizes, few replicates, and high variation gave little power to statistically test for a pond type (spawning vs. nonspawning) effect on growth rate.

The influence from spawning salmon on stream system productivity may not be easily discerned in all stream systems, over broad spatial scales, or in complex natural habitats such as the Copper River Delta. Other studies have documented variation in the responses of salmonids to artificial enrichment (Wilzbach et al. 2005) and in the response of stream biota to natural spawning (Chaloner et al. 2004). The effects of spawning may also be masked in stream systems where responses are limited by other habitat factors, such as canopy coverage (Wilzbach et al. 2005). The ponds that were used in this study were similar in physical characteristics, had open canopies, and no light limitations. However, there may have been high connectivity between the pond types owing to hydrologic and hyporheic flows that would enable nonspawning sites to be indirectly influenced by nutrients from spawning salmon. The nonspawning ponds may also receive salmon-derived nutrients from carcasses through animal transport and floodplain sources (Ben-David et al. 1998; O'Keefe and Edwards 2003). Hicks et al. (2005) found that the concentration of marine-derived nitrogen and carbon in various food organisms of juvenile salmonids in the ponds examined in the current study were similar. This suggests a strong hyporheic connection between ponds in our study system. In nonspawning ponds that may be connected in this manner, the influence from spawning salmon may not result in immediate growth benefits like that associated with direct consumption of eggs and carcasses, but it may affect growth rates and overwinter survival through increased prey abundance and productivity in the ponds over the winter or in the following spring (Wipfli et al. 1998).

At the individual pond level, the enrichment, and to some degree natural spawning, had immediate positive influences on the growth rate and body condition of juvenile coho salmon in the fall. These results are consistent with other studies concerning the influence of spawning on the growth of juvenile salmonids (Bilby et al. 1998; Wipfli et al. 2003). These studies were conducted in small stream habitats and artificial channels. Our study confirms that egg and carcass additions can be successful in boosting the short-term growth of juvenile coho salmon rearing in natural beaver pond habitats as well.

Salmon eggs appeared to be the main resource responsible for increased growth and body condition during enrichment. The diets of fish in the enriched ponds were dominated by eggs (Hicks et al. 2005). During the enrichment, most whole carcasses were intact, with minimal conditioning or decomposition, thus making them unavailable as an immediate food source to juvenile coho salmon. Salmon eggs, on the other hand, were immediately available for consumption by fish in these ponds. Diet analysis of the fish rearing in these ponds confirmed that few juvenile coho salmon consumed carcass flesh during the enrichment (Hicks et al. 2005).

Fish size mattered in the relative influence of enrichment on body condition. Larger fish were of better body condition than smaller fish rearing in the enriched ponds during the enrichment. The most plausible explanation for this result is that the availability and consumption of salmon eggs was greater for larger fish. Larger fish have a greater gape with which to consume eggs, and the larger the fish the more eggs that could potentially be consumed. Smaller fish may consume fewer eggs because of a reduced capacity to swallow an egg. Competition for eggs may also limit the number of eggs available to smaller fish. In feeding experiments,

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Foote and Brown (1998) found that larger sculpins could eat more sockeye salmon (*Oncorhynchus nerka*) eggs than smaller ones. We do not know for sure whether salmonid juveniles were limited in number of eggs consumed or through competition in our study, but these results indicate that competition or lower consumption by smaller fish may have occurred.

The ability to trap juvenile coho salmon dropped substantially during the spawning period. This contrasts with results from other studies where densities increased because fish were attracted to spawning salmon (Bilby et al. 1998; Foote and Brown 1998). In this study, we used minnow traps (a passive method) to capture juvenile coho salmon. The salmon eggs used to bait these traps may not have had enough attractive capacity during spawning because other eggs and food resources may have been plentiful. Electrofishing (Bilby et al. 1998) and visual observation (Foote and Brown 1998) were used to document fish presence on spawning grounds in other studies.

Our study is one of only a few that has documented the response of juvenile salmonids to natural spawning in pristine stream systems where spawning salmon abundance and habitats have not been drastically reduced from historic conditions. Eastman (1996) found that juvenile coho salmon, rainbow trout (*Oncorhynchus mykiss*), and Arctic char (*Salvelinus alpinus*) exhibited increased growth and body condition during spawning by sockeye salmon in the Wood Lakes system, Alaska. In our study, increased growth rates and improved body condition in juvenile coho salmon were generally observed during spawning in ponds with spawning salmon. However, this was not always the case. In pond SP1, the presence of spawning salmon did not confer widespread or detectable benefits to juvenile coho salmon. There were also ponds without spawning that exhibited increased growth and improved body condition relative to before spawning.

There are many reasons why these ponds may not have fit the expected pattern. In a natural system, the full suite of foods and environmental conditions were available to the fish. The highest growth rates of fish observed during the study were from pond SP1 before spawning from August–September 1999. This time period coincides with high rainfall on the Copper River Delta (32.8 cm from 23 August to 15 September, National Oceanic and Atmospheric Administration weather station, Cordova airport). The upper reaches of this system, especially the East Fork consist of high gradient, contained channels that typically result in "flashy" rain and snowmelt events (Blanchet 1983). Flashy streams can benefit fish through frequent flood events that increase availability of drifting invertebrate prey species (Pearson and Franklin 1968) and through access to food resources on floodplains and in side channels (Junk et al. 1989; Giannico and Healey 1998). During sampling in September 1999 at pond SP1, ~3 m of floodplain habitat was accessible to fish on either side of the normal pond bank. Juvenile coho salmon were captured on the floodplains and pond margins and had exceptional body condition and gut fullness. In this case, the short-term benefits of flood-related resource availability might have far outweighed that from spawning salmon.

The presence of Sitka alder may also lessen the dependence of spawning fish as a nutrient source in nonspawning ponds. Sitka alder, a nitrogen fixer, is a dominant component of the riparian plant community around beaver ponds on the Copper River Delta. Alder can represent a major source of nutrients to aquatic communities (Volk et al. 2003) and may be as influential as salmon carcasses in terms of nitrogen enrichment (R.T. Edwards, USDA Forest Service, Pacific Northwest Research Station, 2770 Sherwood Lane, Juneau, AK 99801, USA, personal communication). Alder leaf fall coincides with the arrival of spawning coho salmon on the Copper River Delta and may provide an equal boost in food and nutrient input to the nonspawning ponds.

The fall may also be a time of increased aquatic and terrestrial invertebrate abundance. The diets of fish in the natural spawning and nonspawning ponds were similar and composed mostly of aquatic invertebrates (Hicks et al. 2005). Eggs and carcass material only accounted for a small percentage of the diet of sampled fish in the spawning ponds (Hicks et al. 2005). Corixidae were particularly abundant during spawning in all of the ponds, and they were a major dietary component of juvenile coho salmon in the fall and early winter.

Management implications

This study suggests that enrichment of natural beaver pond habitats with salmon carcasses and eggs can have immediate impacts on the growth rates of juvenile salmonids. Most salmon nutrient restoration efforts have focused on the introduction of carcasses only. To maximize immediate effectiveness for juvenile fish, salmon eggs should be included along with carcasses. Eggs are more readily available and have greater energy content than carcasses. Given the critically low numbers of wild spawning fish (Nehlsen et al. 1991) and the severe disruption of the salmon-derived nutrient linkage of many streams in the Pacific Northwest (Cederholm et al. 1999; Gresh et al. 2000), carcass and egg enrichments may be able to accelerate restoration efforts for some salmon populations.

Fisheries managers should consider the geographic region and the limiting factors associated with the stream system and fish population of interest before incorporating nutrient enrichment projects. Limiting factors such as canopy coverage or overwinter habitat may reduce the potential for carcass and egg enrichments to work. Wilzbach et al. (2005) suggested that in light-limited systems, canopy removals might be more beneficial than enrichment. Enrichment alone may not be enough to increase productivity and smolt abundance in streams with degraded habitats that limit juvenile capacity. Supplemental feeding of coho salmon in a natural stream during the summer increased growth and carrying capacity, but failed to produce greater numbers of smolts the following spring (Mason 1976). Mason (1976) concluded that overwinter habitat limited the number of smolts produced. Some combination of enrichment, stream habitat improvement, and canopy removal may be needesd to restore highly degraded systems.

Gende et al. (2002) noted that it is important to validate experimental results in natural stream environments and to explore potential site- or system-specific variability in the response of freshwater systems to spawning salmon. In our study, the response of juvenile coho salmon to fall-spawning salmon was variable. In most ponds, natural spawning positively influenced short-term growth and body condition in

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the fall, and carcass and egg enrichment greatly increased the growth of fish rearing in ponds that were not naturally exposed to spawning. However, there was little evidence that the short-term benefits observed in the fall led to greater overwinter growth rates or survival to outmigration when compared with fish from ponds that were not directly influenced by spawning salmon in the fall. One potential reason for this result may be that nutrients from spawning salmon are widely distributed across the delta because of hydrologic connectivity and hyporheic flows. There may also be other important factors unrelated to spawning salmon that are important for smolt production. The relationship among spawning salmon, overwinter growth, and smolt production on the Copper River Delta does not appear to be limited to a simple positive feedback loop.

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Conservation and management of exploited shark populations based on reproductive value

Vincent F. Gallucci, Ian G. Taylor, and Karim Erzini

Abstract: Several life history traits of sharks result in juveniles being particularly vulnerable to exploitation. However, population level impacts of harvests on juvenile sharks have not been well quantified. This paper examines a range of harvest strategies, including those targeting juveniles. Reproductive value and yield per recruit are used to compare the harvests, which are represented by Leslie matrix models with a harvest matrix. Two species are used as examples: the short-lived *Rhizoprionodon taylori* and the long-lived *Squalus acanthias*. Harvests that maintain a stationary population size cause reproductive values to change in opposing ways, but they remove equal fractions of the population's reproductive potential. A new theorem gives population growth as a function of the fraction of reproductive potential removed by a harvest, a relationship useful for comparing harvests on juveniles and adults. Stochastic projections indicate that the risk of depletion is associated with the fraction of reproductive potential removed annually, a measure which encompasses the information in both the selectivity and the rate of fishing mortality. These results indicate the value of focusing conservation efforts on preserving reproductive potential.

Résumé : Plusieurs caractéristiques du cycle biologique des requins rendent les jeunes particulièrement vulnérables à l'exploitation. Cependant, les impacts démographiques des récoltes des jeunes n'ont pas été bien mesurés quantitativement. Notre étude examine une gamme de stratégies de récolte, y compris celles qui ciblent les jeunes. La valeur reproductive et le rendement par recrue sont les variables qui nous servent à comparer les récoltes qui sont représentées par des modèles matriciels de Leslie avec un matrice de récolte. Deux espèces servent d'exemple, *Rhizoprionodon taylori*, une espèce à vie courte, et *Squalus acanthias*, une espèce à vie longue. Les récoltes qui maintiennent la taille de la population stationnaire changent les valeurs reproductives de façon opposée chez les deux espèces, mais elles retirent des fractions semblables du potentiel reproductif de la population. Un nouveau théorème présente la croissance de la population comme une fonction de la fraction du potentiel reproductif retirée par une récolte donnée, une relation utile pour comparer les récoltes faites sur les jeunes et les adultes. Des projections stochastiques indiquent que le risque de déplétion est associé à la fraction du potentiel reproductif retirée chaque année, une mesure qui englobe à la fois l'information relative à la sélectivité et aux taux de mortalité due à la pêche. Ces résultats démontrent l'intérêt qu'il y a à concentrer les efforts de conservation sur le maintien du potentiel reproductif.

[Traduit par la Rédaction]

Introduction

It is generally agreed that shark populations are particularly vulnerable to overexploitation because of the limited number of offspring they bear and the long period of time before they are sexually mature (Musick 1999). Merging this line of thought with the standard methodologies applied in fisheries stock assessment leads to a number of inconsistencies. Methods of analysis based on the use of compensatory models such as the Schaefer stock-production model (McAllister et al. 2001) assume that almost all of the life history parameters fundamental to modeling the dynamics can be represented by the two-parameter logistic model. In contrast, age-structured models (Cailliet 1992; Cortés 1998; Punt and Walker 1998) allow the explicit use of the same life history parameters central to understanding why shark populations are easily overexploited. This paper builds on the use of life history parameters by the simultaneous use of the reproductive value of a given species, which is associated with Leslie matrix models (Caswell 2001), and the application of the mathematical methodology of the Beverton and Holt (1957) yield-per-recruit (Y/R) model formulated as a function of reproductive potential removed.

This research was motivated by earlier work on multi-mesh-size artisanal fisheries where juveniles of larger species were captured in mesh sizes designed for smaller species (Lai et al. 1993; Gallucci et al. 1996). In the present case, our initial interest was in sharks that use tropical bays as nurseries (V. Gallucci, personal observation), where artisanal fishermen harvested prereproductive sizes as part of their fishing

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operation. Even if not targeted, sharks were a bycatch item in drift gillnet and seine gear and were either marketed or simply discarded. These harvests of juvenile sharks, which have been noted in other artisanal fisheries (Castillo-Géniz et al. 1998; Kroese and Sauer 1998), led to research into new methods for estimating the impacts of the capture of prereproductive animals in a more generalized context. The traditional approach in stock assessment would attempt to estimate a biological reference point (Gabriel and Mace 1999), which would be an age- or size-specific rate of instantaneous fishing mortality, such as F_{max}, $F_{0.1}$, or F_{MSY}. Occasionally these reference points are based on the spawning stock biomass of the population. The alternative approach we considered was to use reproductive value and the fraction of the reproductive potential of the population removed by harvesting any subset of the ages. This led to the derivation of a new theorem, presented herein.

Reproductive value (RV) has its roots with Fisher (1930) as a part of human demographic analysis and as a part of the ecological literature with MacArthur (1960), who considered fisheries harvests as a special case of optimal foraging theory. He phrased the predator's problem in two ways: when it knows, and does not know, the age of the prey. RV was used in the first case, which also applies to our interest as a fishery typically designs its capture gear to correspond to an initial age of capture. Our work diverges from MacArthur's, but his initial results are a basis for our approach. RV, which can be interpreted as the relative contribution of individuals at each age to the long-term growth of the population, has become a part of demographic analyses like those frequently employed for shark populations (Cailliet 1992; Cortés 1999; Frisk et al. 2002). Reproductive potential (RP) extends RV to the population level. RP is defined here as the sum of RVs of all individuals in a population. This measure, also called "total reproductive value" (Leaman 1987, 1991), was also developed by Fisher (1930) and has been considered as an alternative to spawning stock biomass (Leaman 1987, 1991; Katsukawa et al. 2002). Leaman (1987, 1991) concludes that RP should be incorporated into monitoring programs for decision-making. Taylor and Gallucci (2005) found that the connection between RP and biomass of a species was an indicator of the degree to which surplus production models could fit biomass trends for that species.

Representing the contribution of a shark of a given age to the whole population by its RV allows the quantification of harvest strategies in terms of the removals of these contributions. This approach, used along with Y/R analysis for different exploitation strategies, allows the exploration of the long-term consequences of these harvest policies. By extension, this allows investigation of the balancing of yield, selection of juveniles, and harvest sustainability. Deterministic analyses of the type described above do not provide information on the influence of variability in life history parameters on the results, and so Monte Carlo simulations are used in a risk analysis to supplement deterministic projections.

In this paper, the comparison between short- and long-lived species allows a demonstration of the utility of RV-based measures. The above methodologies are applied to a number of practical situations representing different exploitation scenarios for sharks of two basic types: those that grow to great ages and those that do not. These short- and long-lived types are represented here by the Australian sharpnose shark (*Rhizoprionodon taylori*) and the spiny dogfish (*Squalus acanthias*), respectively. These methodologies allow quantification of the consequences of harvesting prereproductive sharks from nurseries and facilitate tracking the subsequent population wave across the age structure. This analysis demonstrates the potential value of different management approaches for these two archetypes. The RP framework developed here is a valuable new tool for identifying patterns of harvest impacts across life histories and harvest strategies.

Materials and methods

Matrix formulation for harvested populations

Deterministic population dynamics were modeled using age-structured female-only Leslie matrix models (definitions of terms are provided in Table 1). Parameter values (Table 2) were taken from available published information on the Australian sharpnose shark (Simpfendorfer 1999*a*) and the Northeast Pacific population of spiny dogfish (Ketchen 1972, 1975; Saunders and McFarlane 1993). These species were chosen as representative of short- and long-lived species, respectively.

Natural mortality rates for the two species were assumed constant over all ages with $M = 0.561$ for the sharpnose shark (Simpfendorfer 1999*a*). The method of Hoenig (1983) was applied for the dogfish assuming a maximum age of 80 years (McFarlane and King 2003) to get a value of $M = 0.0515$. The annual survivorship terms in the subdiagonal of the Leslie matrix were calculated as $s_x = e^{-M}$.

Length was assumed to follow the von Bertalanffy growth function (Gallucci and Quinn 1979), and average numbers of offspring per mature female was a linear function of length for both species (Table 2). The census for abundance was assumed to be postbreeding (Caswell 2001), making newborn pups the first age class (age 0). The fecundity values thus include the probability of the mother surviving to pup at the end of the year, making possible the modeling of harvests on young-of-the-year pups. A sex ratio of 1:1 was assumed for both species. All sharpnose sharks were assumed to mature at age 1 and to pup every year, whereas mature dogfish were assumed to pup every 2 years. The maturity schedule for dogfish was assumed to be a logistic function of age with 50% maturity at 35.5 years (Saunders and McFarlane 1993), so the fraction mature at age x was $(1 + e^{-0.4(x-35.5)})^{-1}$. The average number of female pups per female of age x, m_x, is the product of the function for the number of pups per mature female (Table 2), the maturity schedule, and the sex ratio. The fecundity terms which make up the first row of the Leslie matrix were calculated as $f_x = s_x m_x$.

Harvests were incorporated into the model as a diagonal matrix **H** following Lefkovitch (1967) and Caswell (2001). The elements of the harvest matrix, h_x, represent the fraction of individuals of age x surviving the harvest. Thus, the usual Leslie age-structured model (Caswell 2001)

$$(1) \qquad \mathbf{N}_{t+1} = \mathbf{M}\mathbf{N}_t$$

where **M** is the projection matrix and $\mathbf{N}_t$ is the vector of numbers at each age in year t, is modified to incorporate age-specific removals of individuals in a harvest:

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Table 1. Definitions of terms.

$\mathbf{M}$	Leslie matrix
$\mathbf{H}$	Harvest survival matrix with diagonal elements h_x
h_x	Fraction surviving harvest at age x
$\mathbf{H}^* = \mathbf{I} - \mathbf{H}$	Diagonal matrix containing fraction harvested at each age with diagonal elements $1 - h_x$
λ	Dominant eigenvalue of $\mathbf{M}$ giving the annual multiplicative increase of the unharvested population at stable age distribution (SAD)
λ'	Dominant eigenvalue of $\mathbf{MH}$ giving the annual multiplicative increase of the harvested population at SAD
$\boldsymbol{w}$	SAD vector for $\mathbf{M}$, satisfying $\mathbf{M}\boldsymbol{w} = \lambda\boldsymbol{w}$
$\boldsymbol{w}'$	SAD vector for $\mathbf{MH}$, satisfying $\mathbf{MH}\boldsymbol{w}' = \lambda'\boldsymbol{w}'$
$\boldsymbol{v}$	Reproductive value vector for $\mathbf{M}$, satisfying $\boldsymbol{v}^{\mathrm{T}}\mathbf{M} = \lambda\boldsymbol{v}^{\mathrm{T}}$
$\boldsymbol{v}'$	Reproductive value vector for $\mathbf{MH}$, satisfying $\boldsymbol{v}'^{\mathrm{T}}\mathbf{MH} = \lambda'\boldsymbol{v}'^{\mathrm{T}}$
v_x	Reproductive value at age x
$P_t = \boldsymbol{v}^{\mathrm{T}}\boldsymbol{N}_t$	Reproductive potential of the population in year t
$P = \boldsymbol{v}^{\mathrm{T}}\boldsymbol{w}'$	Reproductive potential of the SAD vector $\boldsymbol{w}'$ corresponding to $\mathbf{MH}$
$P_h = \boldsymbol{v}^{\mathrm{T}}\mathbf{H}^*\boldsymbol{w}'$	Reproductive potential of the fish harvested from $\boldsymbol{w}'$ each year
$\Phi = P_h/P$	Fraction of the reproductive potential removed by the harvest at SAD
$\boldsymbol{N}_t$	Vector of numbers at each age in year t
$N_{x,t}$	Number of individuals of age x in year t
t_c	Age of entry into the fishery
t_s	Maximum age selected by the fishery
t_m	Maximum age of the species

Table 2. Parameter values used for each species.

Species	Common name	Pups per mature female (TL in cm)	Age of 50% maturity	t_m	M	L_∞	K	t_0
Rhizoprionodon taylori	Australian sharpnose shark	0.19·TL – 7.919	1	7	0.561	73.2	1.013	–0.455
Squalus acanthias	Spiny dogfish	0.20·TL – 13.24	35.5	80	0.0515	114.94	0.0437	–3.557

Note: TL, total length; M, natural mortality; L_∞, K, t_0, standard von Bertalanffy growth function parameters. See Table 1 for other definitions.

$$\boldsymbol{N}_{t+1} = \mathbf{MH}\boldsymbol{N}_t \quad (2)$$

The augmented projection matrix **MH** has the same form as the Leslie matrix but fecundity and survival of the harvested ages are reduced. The dominant eigenvalue of **M**, λ, and, the dominant eigenvalue of **MH**, λ′, give the asymptotic annual change in population size with and without a given harvest. Primed (′) variables are associated with a harvested population. Thus, the unharvested case (eq. 1) is a special case of eq. 2.

Two general classes of harvest strategy were evaluated: juvenile and adult. The selection of a younger portion of the population is intended to represent harvests on the juvenile population present in nursery areas or the only sizes available to artisanal fishers. The selection of the older portion of the population matches the more common pattern of minimum size limits or the use of selective gear in commercial fisheries. For juvenile harvests, the age of entry into the fishery t_c was set to 0, and for adult harvests, the maximum age in the fishery t_s was set to the maximum age for the species, t_m (Fig. 1). All individuals between t_c and t_s are considered fully recruited into the fishery.

To reduce the set of harvests considered, the fraction harvested annually from all selected ages was equal. Thus, the harvest matrix **H** has diagonal elements $h_i = h$ for $t_c \le i \le t_s$ and $h_i = 1$ otherwise. The harvest rate ($1 - h$), associated with a stationary population size, was found by iteratively searching for the constant survival fraction h, which made $\lambda' = 1$. The term "stationary harvest" will be used for all harvests that make $\lambda' = 1$. The right and left eigenvectors corresponding to these eigenvalues give the reproductive value and the stable age distribution, respectively.

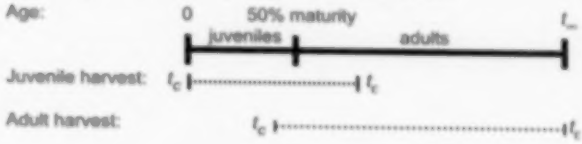

Fig. 1. Example of juvenile and adult harvests showing that both types may include some juveniles and some adults.

RV and stable age distribution

The RV vector $\boldsymbol{v}$ was calculated as the right eigenvector of the projection matrix **M**, satisfying

$$\boldsymbol{v}^{\mathrm{T}}\mathbf{M} = \lambda\boldsymbol{v}^{\mathrm{T}} \quad (3)$$

where $\boldsymbol{v}^{\mathrm{T}}$ is the transpose of the column vector $\boldsymbol{v}$. The RV of the harvested population $\boldsymbol{v}'$ is the right eigenvector of **MH**, satisfying

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(4) $\mathbf{v}'^{\mathrm{T}}\mathbf{MH} = \lambda'\mathbf{v}'^{\mathrm{T}}$

The resulting elements of $\mathbf{v}$, which are defined by eq. 4 only up to a scalar multiplier, are proportional to those given by the discrete form of Fisher's (1930) formula:

(5) $$v_x = \sum_{i\geq x} \lambda^{-(i-x)} f_i \frac{l_i}{l_x}$$

where v_x is the RV at age x, and $l_x = \prod_{i=0}^{x-1} s_i$ is the probability of survival from birth to age x. The elements of $\mathbf{v}'$ can be calculated using eq. 5 by substituting λ', f_x', and l_x' derived from the augmented projection matrix **MH**.

Evaluating eq. 5 at $x = 0$ yields a function similar to the Euler–Lotka equation (Lotka 1907). This similarity can be used to show that computing v_x using eq. 5 is equivalent to scaling the $\mathbf{v}$ so that $v_0 = \lambda$. Correspondingly, harvests that lead to a stationary population size have $v_0' = \lambda' = 1$. Under such stationary harvests, eq. 5 is identical to the equation for life-time egg production of an individual of age x (Quinn and Deriso 1999):

(6) $$R_x = \sum_{i\geq x} f_i \frac{l_i}{l_x}$$

so that the net reproductive rate R_0 will equal the reproductive value at age 0: $R_0 = v_0' = 1$. The scaling of the eigenvectors to make $v_0 = \lambda$ and $v_0' = \lambda'$ has been used when comparing v_0 and v_0'.

The stable age distribution (SAD) vectors of unharvested and harvested populations, $\mathbf{w}$ and $\mathbf{w}'$, are the left eigenvectors corresponding to λ and λ' (Caswell 2001), respectively, and satisfy

(7) $\mathbf{Mw} = \lambda\mathbf{w}$

and

(8) $\mathbf{MHw}' = \lambda'\mathbf{w}'$

Reproductive potential

RP, a scalar value, is defined here as the sum of the RVs of all individuals in the population, whether at a SAD or not. It is computed following Leslie (1948) as the vector inner product

(9) $$P_t = \mathbf{v}^{\mathrm{T}}\mathbf{N}_t = \sum v_x N_{x,t}$$

where $N_{x,t}$ is the element of the population vector $\mathbf{N}_t$ corresponding to age x. RP is a measure of the potential for the population to grow in the absence of a harvest. Thus, $\mathbf{v}$ rather than $\mathbf{v}'$ is used in eq. 9.

The RP of the SAD vector $\mathbf{w}'$ is given by

(10) $P = \mathbf{v}^{\mathrm{T}}\mathbf{w}'$

and the RP of the portion of this population that is removed by the harvest in each year is

(11) $P_h = \mathbf{v}^{\mathrm{T}}\mathbf{H}^{\circ}\mathbf{w}'$

where $\mathbf{H}^{\circ} = (\mathbf{I} - \mathbf{H})$, with $\mathbf{I}$ the identity matrix, is the diagonal matrix containing the fraction of each age removed by the harvest. The ratio of these two quantities gives the fraction of the reproductive potential removed by a stationary harvest at SAD:

(12) $\Phi = P_h/P$

Yield per recruit

Y/R was calculated for a range of harvest strategies as

(13) $$\mathrm{Y/R} = \sum_{x=0}^{t_m} (1 - h_x) l_x' W_x$$

where $(1 - h_x)$ is the probability of being harvested at age x, $l_x' = \prod_{i=0}^{x-1} s_i h_i$ is the fraction of the cohort surviving to age x under the harvest, and W_x is the weight at age x given by the von Bertalanffy growth equation. The fraction surviving the harvest was also converted to a rate $F = -\ln(h)$, which was used in the Beverton–Holt Y/R model (Beverton and Holt 1957). A comparison between eq. 13 and the Beverton–Holt model found similar results, with small differences resulting from the alternative treatments of growth and mortality as discrete or continuous processes.

Y/R was calculated for adult harvests over a two-dimensional grid of the fraction of RP removed by the harvest each year (Φ) vs. age of entry (t_c) values with the maximum age in the fishery (t_x) fixed at the maximum age of the species (t_m). The parameters in the grid for juvenile harvests were Φ and t_c, with $t_c = 0$. The value of $h_x = h$ for a given range of ages $t_c \leq x \leq t_x$ that corresponded to Φ was found using an iterative search.

Stochastic projections and risk

The augmented projection matrix **MH** is a deterministic model of population dynamics under given fecundity and survival parameters, along with harvests of selected ages. The risk of depletion per harvest strategy was evaluated by including stochasticity in the survival, fecundity, and harvest parameters. Fecundity was assumed to have a lognormal distribution around a mean, f_x. The instantaneous rates $M = -\ln(s_x)$ and $F = -\ln(h)$, were also assumed lognormal. Use of the lognormal distribution for the instantaneous rates is convenient because the resulting fractions for survival and harvest will be between 0 and 1. The stochastic elements of the projection and harvest matrices for age x in year t were calculated as $\tilde{f}_{x,t} = f_x \varepsilon_t$, $\tilde{s}_{x,t} = e^{-M\delta_t}$, and $\tilde{h}_t = e^{-F\gamma_t}$, where ε_t, δ_t, and γ_t are all lognormal random variables with mean = 1 and coefficient of variation (CV) = 0.2. The same random variables were applied to all ages under the assumption that environmental effects will have similar impacts on all ages. Conditions that increased fecundity were assumed to decrease natural mortality, on average, so ε_t and δ_t were negatively correlated, with coefficient $\rho = -0.5$.

A harvest strategy is defined by specification of t_c, t_x, and either the fraction of the total RP removed in each year, Φ, or the fraction of the total biomass removed each year, β. The harvest survival parameter h corresponding to Φ or β was calculated in each year as

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$$(14)\quad h = \begin{cases} 1 - \Phi \dfrac{\sum_{x=0}^{t_x} N_{x,t} V_x}{\sum_{x=t_c}^{t_x} N_{x,t} V_x} & \text{when } \Phi \text{ is specified} \\ 1 - \beta \dfrac{\sum_{x=0}^{t_x} N_{x,t} W_x}{\sum_{x=t_c}^{t_x} N_{x,t} W_x} & \text{when } \beta \text{ is specified} \end{cases}$$

For each harvest strategy, 1000 stochastic projections were made in which an initial population at SAD, with biomass B_0, was projected forward 50 years to determine a final biomass B_{50}. The probability that a projection ended below 20% of the initial biomass, $P(B_{50} < 0.2B_0)$, was used as an estimate of the risk of depletion associated with each harvest strategy.

Results

Changes in reproductive value

Changes in RV differed under juvenile and adult harvests and between species (Fig. 2). These RVs may be interpreted as the relative contribution of individuals at each age to the long-term growth of the population under different harvest conditions. The bold lines in Fig. 2 refer to the RVs of the unharvested population of each species. All harvests are designed to maintain a stationary population size by constraining the removal of the selected ages so that $\lambda' = 1$. Under these harvests, the population may exhibit dampened oscillations as it approaches the SAD associated with the projection matrix **MH**, but at that SAD, the population size will be constant, regardless of the initial age distribution and population size.

The changes in RV under harvests on different segments of the population were unexpected: harvests that target juveniles can increase RV above the level corresponding to no harvest. Although unexpected, an explanation is available. In all cases, harvests reduce survival of the harvested ages. Any harvest will reduce λ' below λ, but when only juveniles are selected into the fishery, survival and fecundity of adults are unaffected. Thus, if λ', f_x', and l_x' are substituted into the summation equation for RV (eq. 5), the negative exponent on λ' will result in an increase in RV at all ages older than those selected into the fishery because the ratio l_x'/l_s' will be unaffected by the harvest on younger ages. The RV of some juvenile ages selected into the fishery decreases because the impact of the harvest on survival and fecundity is more influential than the changes in λ'. In general, the adult ages that are unaffected by a harvest on juveniles and are already producing offspring are relatively more valuable to the population than the juveniles being harvested.

Harvests on adults, in contrast, reduce the RV of all ages in the population. The eigenvalue λ' is again reduced, but unlike harvests on juveniles, harvests that reduce the survival and fecundity of adults will impact the RV of all ages. Larger reductions occurred at the ages selected into the harvest, but because RV is a sum over all expected future offspring, the impact of a harvest on the last age in the population will reduce RV of all prior ages as well. The harvests associated with the greatest reductions in RV for both species considered were those targeting the smallest number of adult ages. The harvest rates associated with these harvest strategies (Tables 3 and 4) are the highest among the strategies considered under the constraint $\lambda' = 1$. Thus, the low RV associated with harvests on the oldest segment of the population may be interpreted as a measure of the high harvest rates, which may be applied to the oldest fish while maintaining a stationary population size.

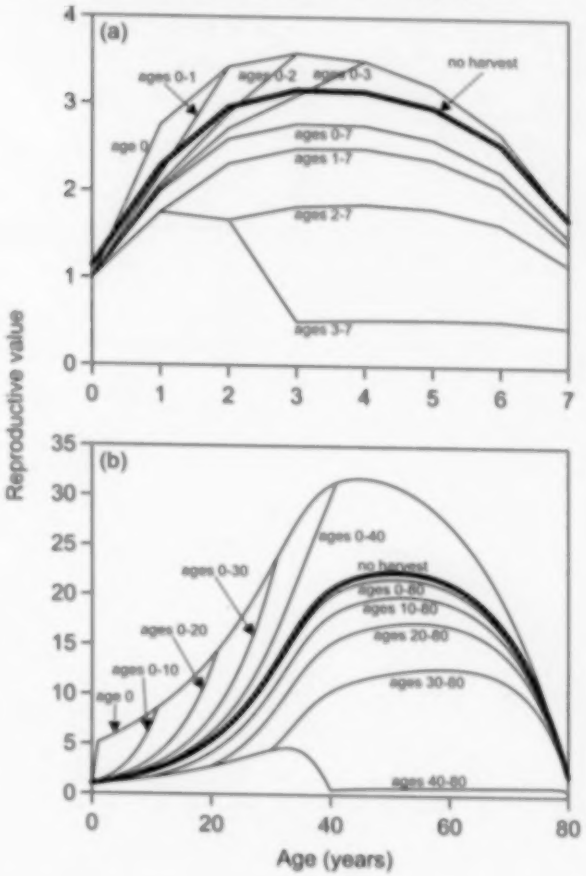

Fig. 2. Reproductive value vs. age for (*a*) *Squalus acanthias* and (*b*) *Rhizoprionodon taylori* under harvests that maintain a stationary population size and under no harvest. Labels denote the range of ages selected into the harvest for each curve.

Population growth

Details are given of the harvests considered under the constraint that they will lead to a stationary population size ($\lambda' = 1$) (Tables 3, 4). Harvests on adults may target more ages or remove a greater fraction ($1 - h_x$) of each targeted age while maintaining a stationary population size. The differences in sustainable harvest rates between strategies are an indication of the interdependence between selectivity and sustainable harvests. The fraction of a population's biomass that may be sustainably removed each year is a function of

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Table 3. Details of stationary harvests for *Rhizoprionodon taylori*.

Type of harvest	t_c	t_r	Harvest fraction $(1 - h_v)$	F	λ'	R_0	Y/R	Φ	β	Fraction of numbers harvested
No harvest	—	—	0	0	1.141	1.572	0	0	0	0
Juvenile	0	0	0.364	0.452	1	1	0.018	0.124	0.029	0.199
Juvenile	0	1	0.202	0.226	1	1	0.052	0.124	0.079	0.153
Juvenile	0	2	0.155	0.168	1	1	0.070	0.124	0.102	0.135
Juvenile	0	3	0.137	0.147	1	1	0.078	0.124	0.113	0.128
All ages	0	7	0.124	0.132	1	1	0.087	0.124	0.124	0.124
Adult	1	7	0.174	0.191	1	1	0.120	0.124	0.162	0.090
Adult	2	7	0.311	0.372	1	1	0.139	0.124	0.183	0.079
Adult	3	7	0.731	1.313	1	1	0.148	0.124	0.193	0.076

Note: F, fishing mortality; R_0, net reproductive rate; Y/R, yield per recruit; β, fraction of the total biomass removed each year. See Table 1 for other definitions.

Table 4. Details of stationary harvests for *Squalus acanthias*.

Type of harvest	t_c	t_r	Harvest fraction $(1 - h_v)$	F	λ'	R_0	Y/R	Φ	β	Fraction of numbers harvested
No harvest	—	—	0	0	1.032	4.892	0	0	0	0
Juvenile	0	0	0.7956	1.588	1	1	0.019	0.0314	0.0026	0.1656
Juvenile	0	10	0.1344	0.144	1	1	0.117	0.0314	0.0149	0.0926
Juvenile	0	20	0.0728	0.076	1	1	0.239	0.0314	0.0267	0.0623
Juvenile	0	30	0.0500	0.051	1	1	0.328	0.0314	0.0309	0.0464
Juvenile	0	40	0.0389	0.040	1	1	0.378	0.0314	0.0309	0.0375
All ages	0	80	0.0314	0.032	1	1	0.432	0.0314	0.0314	0.0314
Adult	10	80	0.0397	0.041	1	1	0.533	0.0314	0.0353	0.0182
Adult	20	80	0.0547	0.056	1	1	0.593	0.0314	0.0327	0.0117
Adult	30	80	0.0935	0.098	1	1	0.587	0.0314	0.0281	0.0083
Adult	40	80	0.7059	1.224	1	1	0.620	0.0314	0.0261	0.0071

Note: F, fishing mortality; R_0, net reproductive rate; Y/R, yield per recruit; β, fraction of the total biomass removed each year. See Table 1 for other definitions.

the ages selected by the harvest, where a greater fraction of the biomass is sustainably removed via harvests of adult ages of the two species. Unlike biomass, the fraction of a population's reproductive potential Φ that may be sustainably removed each year is independent of the ages selected by the fishery. This is demonstrated in the following theorem and lemma.

Theorem: (Taylor, Gallucci) The asymptotic annual growth of a harvested population λ' decreases linearly with the fraction of the reproductive potential harvested Φ annually:

$$\lambda' = \lambda(1 - \Phi) \quad (15)$$

Proof:

$\lambda' = \lambda' v^T w'/P$ — multiplying λ' by a fraction equal to 1, using eq. 10

$= v^T \lambda' w'/P$ — λ' is commutative under multiplication with v^T

$= v^T \mathbf{M}\mathbf{H} w'/P$ — substitution using eq. 8

$= \lambda v^T \mathbf{H} w'/P$ — substitution using eq. 3

$= \lambda(v^T w' - v^T \mathbf{H}^+ w')/P$ — substituting $\mathbf{H}^+ = (\mathbf{I} - \mathbf{H})$ and distributing

$= \lambda(P - P_h)/P$ — definitions of P and P_h

$= \lambda(1 - \Phi)$ — distributing $1/P$ and substituting $\Phi = P_h/P$

Lemma: If the fraction of reproductive potential annually removed by the harvest is $(\lambda - 1)/\lambda$, then the population size will be stationary when it reaches SAD.

Proof: Substituting $\Phi = (\lambda - 1)/\lambda$ into eq. 15 gives

$$\lambda' = \lambda(1 - \Phi)$$
$$= \lambda(1 - (\lambda - 1)/\lambda)$$
$$= 1$$

If the Perron–Frobenius theorem (Caswell 2001) applies to $\mathbf{M}$, then under ordinary harvests (no removal of 100% of any age class), it will apply to $\mathbf{MH}$ and the population will approach a SAD. Having $\lambda' = 1$ will result in a stationary population size when the population reaches SAD. The linear relationship between λ' and Φ is shown (Fig. 3).

The results of both the theorem and lemma are independent of the ages selected by the harvest. The only effect of the selectivity pattern is that there may be a maximum Φ associated with harvests on adults. The value $\Phi = (\lambda - 1)/\lambda$, which leads to a stationary population size for a given set of demographic parameters, will be denoted $\Phi_{stationary}$. The values corresponding to the two species are $\Phi_{stationary} = 0.124$ for the sharpnose shark and $\Phi_{stationary} = 0.031$ for the dogfish. The lower level of removals that can be sustained by the dogfish are characteristic of long-lived elasmobranchs (Hoenig and Gruber 1990). Although the increase in population size per generation of dogfish is actually higher, their long generation time results in a very low annual increase in

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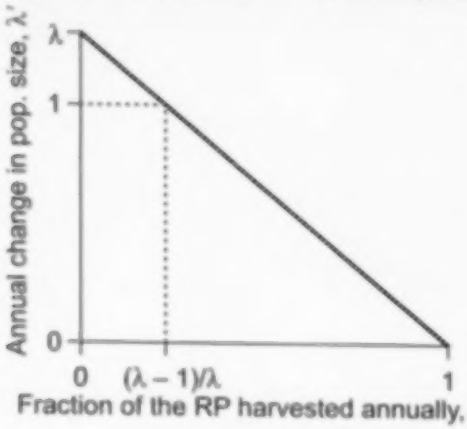
Fig. 3. The relationship between λ' and Φ as given by the theorem and lemma. Pop., population; RP, reproductive potential.



population size ($\lambda = 1.032$). Although it is intuitive that sustainable levels of fishing pressure are related to a population's growth rate, this theorem provides a quantitative framework for calculating the fraction of a population's reproductive potential that may be sustainably harvested each year.

The theorem implies that expressing effort in terms of the fraction of RP removed from the population each year is the most accurate indicator of the impact of that harvest on the growth of the population. Because λ' is directly related to Φ, a harvest that removes a greater fraction of the RP annually will have a larger impact on λ', regardless of the selectivity pattern of the fishery. Two instantaneous rates of fishing mortality can only be compared in this way when they are applied to the same selected age classes. For this reason, fishing effort in the following Y/R calculations was described in terms of the fraction of RP removed annually by the harvest.

Yield per recruit

Expressing fishing effort in the Y/R analysis in terms of Φ, the fraction of RP removed from the population each year, makes comparison of Y/R among sustainable harvests easy (Fig. 4). A vertical line at $\Phi_{stationary} = (\lambda - 1)/\lambda$ indicates those harvests that lead to a stationary population size, as shown in the lemma above. Some levels of removal were not possible for some adult harvests, in which case no Y/R was calculated. If the fraction of the RP contained within cohorts of age t_c and older is less than a given Φ, then no harvest on ages t_c and older can remove a fraction of RP equal to Φ. The t_c values for which no Φ above the stationary harvest rate can be removed are very conservative harvest strategies. In these ranges ($t_c \geq 3$ for sharpnose shark and $t_c \geq 40$ for the dogfish), the population will not be depleted under any amount of fishing pressure.

Considering changes in t_c or t_0 corresponding to $\Phi_{stationary}$, maximum Y/R from juvenile harvests occurred when the harvest included all adult ages in addition to juveniles. Maximum Y/R from stationary adult harvests was higher than Y/R from any juvenile harvest. For the sharpnose shark, this maximum occurred when the age of entry into the fishery was as high as possible ($t_c = 3$ in Fig. 4*a*). With the dogfish, Y/R for stationary harvests was highest with $t_c = 24$ years (Fig. 4*b*). For both species, the highest Y/R at sustainable levels of Φ was about 50% higher among adult harvests than among juvenile harvests and about 100% higher among adult harvests than among juvenile harvests that included no adults.

The short-lived sharpnose shark has a high natural mortality rate ($M = 0.561$) that is unlikely to be approached by any fishing mortality rate. Therefore, within the range of Φ considered, an increase in fishing effort applied to any range of harvested ages will increase Y/R because decreases in a cohort resulting from natural mortality will be faster than increases in weight. The peak Y/R occurs at the maximum possible Φ for the harvests on adults, whereas for juveniles, the peak Y/R occurs around $\Phi = 0.4$, when the population is declining sharply already. For this species, the concern is avoiding recruitment overfishing by removing RP only from older ages that have had more time to reproduce. In contrast, natural mortality for the dogfish and other long-lived sharks is low enough that it may easily be matched or surpassed by fishing mortality. In this case, growth overfishing is also a concern. That is, especially for harvests on juveniles, increasing the fraction of RP removed from any range of ages will decrease Y/R through a shift in the mean age of harvested individuals toward the age of entry in the fishery. These younger individuals, which weigh less, would have had a high probability of surviving to an older, heavier age with less fishing pressure. For dogfish, the peak Y/R from juvenile harvests is close to the stationary harvest level. Thus, in addition to indicating the advantage of adult harvests over juvenile harvests for both species, the Y/R analysis shows that for a long-lived species, in addition to decreasing recruitment, the Y/R will be adversely impacted by overfishing.

Stochastic projections and risk

For both species, the risk of population depletion, defined as the probability that a 50-year stochastic projection will end below 20% of the initial biomass, $P(B_{50} < 0.2B_0)$, was similar for all harvest strategies at any given removal of RP, Φ (Figs. 5*a*, 5*b*), but the risk associated with a given removal of biomass, β, was highly dependent on the range of ages harvested (Figs. 5*c*, 5*d*). For the short-lived sharpnose shark (Fig. 5*a*), $P(B_{50} < 0.2B_0)$ rose from less than 0.05 at $\Phi = 0.11$ to greater than 0.95 at $\Phi = 0.16$. For ages 3–7, many projections resulted in a fraction of RP contained in these ages less than Φ, so the risk presented is the result of removing all individuals from these ages in some years. In contrast, when harvests are described in terms of removals of biomass (Fig. 5*c*), a harvest of only 5% from age 0 caused all projections to fall below $0.2B_0$, whereas three times as much biomass could be removed from ages 2–7 or ages 3–7 without causing such depletion in most of the projections.

For dogfish, the transition from low to high risk occurs over a narrower range of Φ (Fig. 5*b*). The late age of maturity and long lifespan of dogfish means that stochastic fecundity will impact only one or two generations in the 50-year projections, so the impact of a series of good or bad years on the variability in the projections is reduced. This lower variability in stochastic projections for the longer-lived species is also consistent with the results of Goodman (1984). None of the projections for dogfish fell below $0.2B_0$ at $\Phi = 0.05$,

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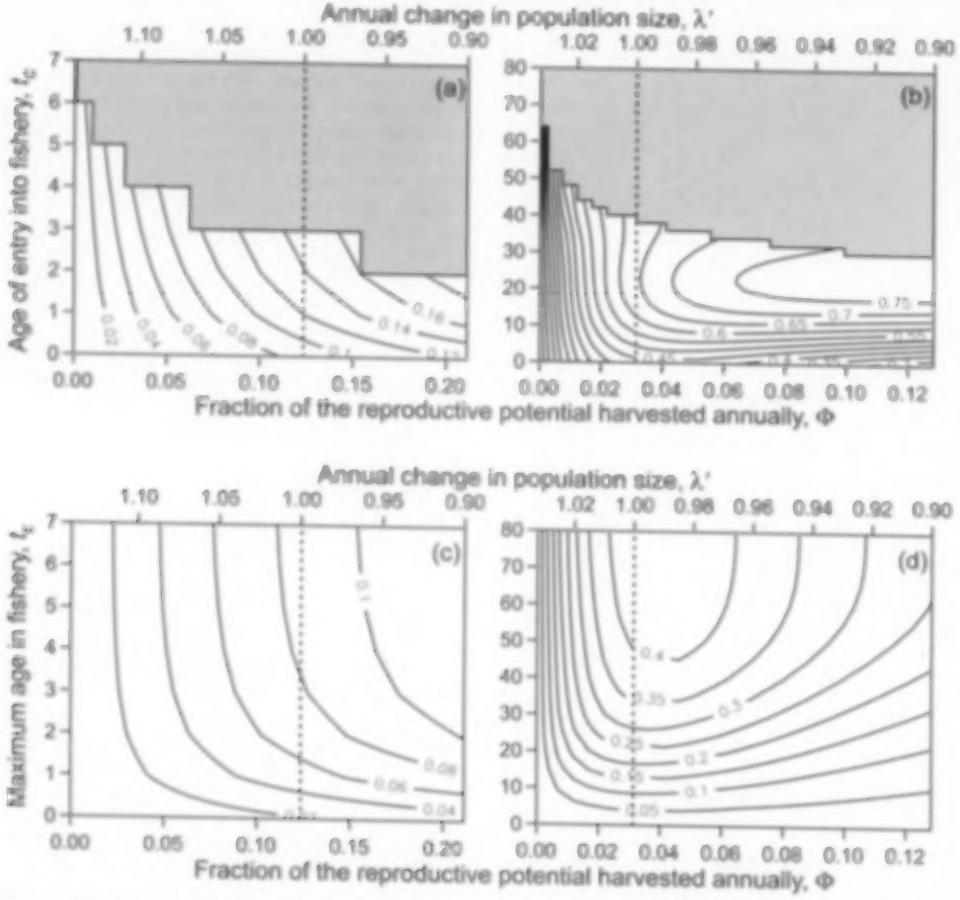
Fig. 4. Isopleths of yield per recruit as a function of selectivity parameters and fishing pressure expressed as Φ, the fraction of reproductive potential (RP) harvested each year. The corresponding annual change in population size λ' is shown at the top of each figure. (*a*) Adult harvests on *Rhizoprionodon taylori*; (*b*) adult harvests on *Squalus acanthias*; (*c*) juvenile harvests on *Rhizoprionodon taylori*; (*d*) juvenile harvests on *Squalus acanthias*. The vertical lines mark $\Phi_{stationary} = (\lambda - 1)/\lambda$, the value of Φ that leads to a stationary population in a deterministic projection. Shading indicates the fraction of RP in selected ages that is less than Φ.



but at $\Phi = 0.08$, all projections fell below this level with the exception of strategies that led to removal of 100% of some ages.

When the harvest level on dogfish was based on the fraction of biomass removed from the population (Fig. 5*d*), the risk was highly dependent on the range of ages selected by the harvest, as with the sharpnose shark. The risk of population depletion was again highest when harvests targeted only juveniles (ages 0–10, 0–20, and 0–30). The harvest targeting the old ages (ages 40–80) was again the most conservative and did not lead to any populations below $0.2B_0$, even when all individuals in these ages were harvested. Harvests on age 0 likewise did not lead to depletions, indicating that if a harvest is going to take place on juveniles, then a very narrow slot limit will reduce the risk of depletion.

In this stochastic framework, Φ is the fraction of observed RP removed in each year, rather than the fraction removed at SAD. However, the connection between risk of population depletion and Φ, independent of the ranges of ages selected by the harvest and in contrast to the more complex relationship between risk of depletion and the fraction of biomass removed, further indicates the utility of using Φ as a measure of the impact of a harvest.

Discussion

RV and RP are applied to the dynamics of harvested shark populations. The argument made here is that the fraction of RP removed from a population is more representative of the impact of harvesting on a population than the traditional instantaneous rate of fishing mortality or other related management tools. This argument is supported by the results above.

MacArthur (1960) discusses RV and removals from a population in the context of optimal predation. He suggests that an optimal predator will remove individuals from the population from those ages that maximize the ratio: value to predator vs. reproductive value. Working with a continuous time model, he also considered the allowable rate of removals. This work was extended by a large body of literature on

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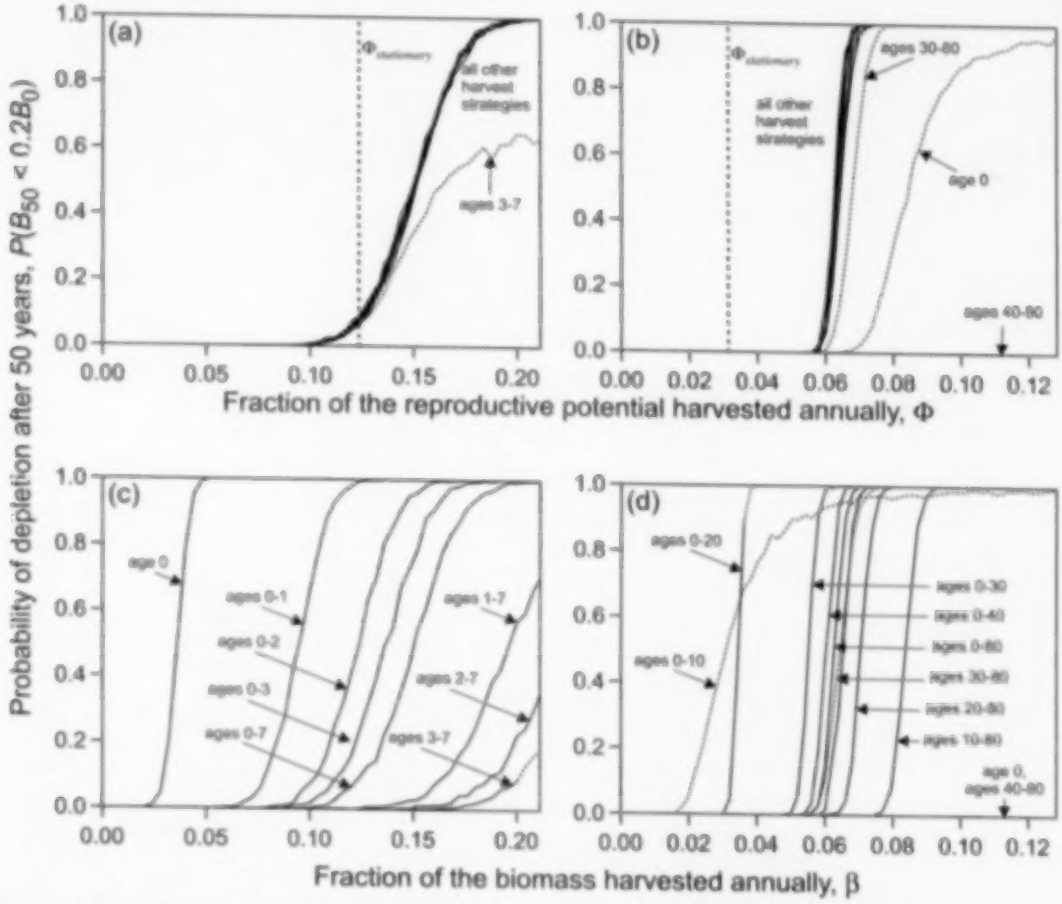
Fig. 5. Risk of severe depletion associated with different levels of harvest, as a function of harvesting (*a*) reproductive potential from *Rhizoprionodon taylori*, (*b*) reproductive potential from *Squalus acanthias*, (*c*) biomass from *Rhizoprionodon taylori*, and (*d*) biomass from *Squalus acanthias*. Labels denote the range of ages selected into the harvest for each curve. Dashed sections of the risk curves indicate that over 90% of the projections led to complete removal of some ages classes. The vertical lines in (*a*) and (*b*) mark $\Phi_{stationary} = (\lambda - 1)/\lambda$, the value of Φ that leads to a stationary population in a deterministic projection. Arrows pointing to figure boundaries indicate risk curves that are constant at 0.



optimal harvests (Beddington and Taylor 1973; Law 1979; Brooks and Lebreton 2001). However, the gear selectivity required for optimal harvests as defined in these papers is unrealistic in most fisheries contexts. The optimal harvest in these papers involves targeting at most two age classes. In contrast, we provide no formulae for optimizing harvest, but instead provide tools for exploring the consequences of different harvest strategies. Goodman (1982) reiterated the more generally applicable idea of MacArthur (1960) that removals from a population should be measured in units of reproductive value lost. Almost a half century after MacArthur, this paper presents new uses of reproductive potential as a measure of fishing effort and a new theorem regarding the connection between the rate of population growth and removals of reproductive potential. It has also been suggested that the proof provides a rigorous foundation for MacArthur's (1960) paper.

The use of RV and RP and their applications comes from the use of the Leslie matrix and its augmented form with a harvest matrix. In our formulation, a harvested population projected with the augmented Leslie matrix will converge to a SAD. Asymptotic stationarity of the harvested population was accomplished by constraining the dominant eigenvalue of the augmented matrix (λ') to 1. With $\lambda' = 1$, populations will converge to a SAD, at which point the population size will be stationary.

The theorem in this paper states that the growth of a population projected by the augmented Leslie matrix is directly linked to the fraction of RP removed from the population, Φ. This holds regardless of the segment of a population that is harvested. A non-zero Φ corresponds to a range of yields, which are associated with a variety of harvest strategies. The reformulation of the Beverton–Holt Y/R model as a function of Φ and the age of entry into the fishery, t_c, or the maximum age in a juvenile harvest, t_p, provides Y/R isoclines that will look familiar to a stock assessment scientist. It is easy to compare Y/R for the different strategies that lead to stationary harvests as they all correspond to the same value of Φ.

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The approach used here shares some properties with elasticity analysis (Caswell 2001), which has been used extensively in the elasmobranch literature (Heppell et al. 1999; Cortés 2002; Mollet and Cailliet 2002). Although mathematically related, RP differs from elasticity in important ways. Both make use of RV to identify the relative vulnerability of a population to impacts on different population segments. However, whereas elasticity is a measure of the Leslie matrix only, RP combines RV from the Leslie matrix with the numbers-at-age in the population. Therefore, RP can be used to track changes in a population over time (Leaman 1987, 1991; Katsukawa et al. 2002). Also, although elasticity can provide an approximation to the effect of a given harvest (Caswell 2001), the theorem in this paper linking population growth directly to the removal of RP allows the use of the fraction of RP removed, Φ, as an alternative measure of fishing effort.

Any application of this theorem and associated theory must rest on two different aspects of the real world: density-dependent effects and stochastic environments. Density dependence was not considered in this analysis for two reasons. First, the insight found in considering simpler models should provide a platform on which to build further research as our understanding of density dependence in elasmobranchs (Smith et al. 1998) increases. Second, a population kept at a given size will have constant survival and recruitment even in density-dependent models. Therefore, the problem of keeping the population stationary at any particular size in a density-dependent model is equivalent to the density-independent problem of maintaining a stationary population with the corresponding set of population parameters (Quinn and Szarzi 1993). That the implications of the theorem also apply outside the deterministic framework is indicated by the results of the risk analysis in which removal of RP was directly linked to the probability of population depletion. The next two sections compare the use of RV and RP.

Reproductive value

The term reproductive value has connotations of a measure that should be preserved or even maximized. Indeed, the equivalence between maximizing fitness (measured by λ) and maximizing RV has been debated in a series of papers on optimal life history strategies (Schaffer 1974; Yodzis 1981; Caswell 1982). All harvests in the density-independent model used in this paper reduce the dominant eigenvalue and thus reduce fitness as it is defined in the optimal life history literature. When a range of ages that includes juveniles is harvested from either species, the RV for some ages increases above the level associated with no harvest. However, when a single age is harvested, the RV of that one age is below the unharvested level, even if the RV of other ages is above. This is a consequence of both the constraint that all harvests result in a stationary population size and the strongly nonlinear relationship between RV and the harvest matrix parameters. These results are consistent with those of Yodzis (1981) that maximizing fitness is equivalent only to RV maximized with respect to the reproductive effort at a given age but not with respect to reproductive effort of all ages. In the results above, decreases in the eigenvalue of the augmented matrix correspond to decreases in the RV of a single harvested age, but not decreases in RV of all ages simultaneously.

The contrast between changes in RV associated with juvenile harvests and those associated with adult harvests suggests that changes in RV, especially for the older ages, are not good indicators of the effect of a harvest on the potential for growth of a population. Without more information than RV, such as the age distribution of the population, the effect of a harvest cannot be evaluated. Two harvests that are constrained to maintain stationary population sizes may lead to opposite effects on the RV of some ages. It follows that RP, as a sum of the unharvested RV over all individuals in the population, has the potential to be a better indicator of the impacts of a harvest because it includes information about the age distribution.

Reproductive potential

The framework presented in this paper is applicable to a wide variety of species. We focused on shark populations because they are harvested, they range greatly in longevity, and they are the objects of considerable conservation interest. The RP framework was used here to demonstrate that the short-lived Australian sharpnose shark was more susceptible to recruitment overfishing than growth overfishing, whereas the long-lived spiny dogfish is susceptible to both growth overfishing and recruitment overfishing, especially when juveniles are selected into the fishery. For both species, juvenile harvests lead to a greater risk of depletion than harvests that remove the same fraction of the population's biomass from adults. This pattern holds for both species and is likely to be characteristic of shark populations in general. Thus, the intuitive guideline that harvesting of juveniles endangers a population has here been given a mathematical foundation. These results also highlight one concern over the use of surplus production models, because the impacts of a suggested harvest rate may be highly dependent on the range of ages harvested.

Although only two species were considered here, and the knife-edged selectivity functions considered in the paper are only an approximation to true selectivity patterns, the benefits in yield and reduction in risk associated with harvesting the oldest possible segment of the population likely apply to many shark fisheries. Exceptions to this general rule may occur when the range of ages selected by a juvenile fishery is very narrow. In such gauntlet fisheries (Simpfendorfer 1999*b*), only high levels of effort would remove too much reproductive potential from the population. Likewise, for species where the oldest individuals are found to be the most successful spawners, the RV would reflect this, and lower fishing pressure on these oldest ages might be preferred. However, when a fishery, either artisanal or commercial, does harvest juveniles, any concurrent harvest of adults likely imperils the population.

In addition to demonstrating the benefits of avoiding harvests on juvenile sharks, the analyses in the paper have shown the utility of measures based on RP. Although survival and fecundity rates for an individual species are required to compute RV and RP, the analysis of long- and short-lived shark species identified similar trade-offs between sustainable yield and the selection of juveniles. These patterns may be used to guide the management of fisheries on species for which less information is available.

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Simulating and testing the sensitivity of ecosystem-based indicators to fishing in the southern Benguela ecosystem

Morgane Travers, Yunne-Jai Shin, Lynne Shannon, and Philippe Cury

Abstract: The sensitivity of size-based, species-based, and trophodynamic indicators is examined for the fish community of the southern Benguela ecosystem (South Africa) through simulations of different fishing scenarios using the multispecies model OSMOSE. The simulations suggest that it may be erroneous to consider one absolute reference direction of change for any indicator because the direction of change is specific to both the multispecies assemblage and the fishing scenario considered. The analysis of species versus community indicators is helpful for understanding which processes drive the emergent properties of the ecosystem. Informative about the structure and state of the ecosystem, both types of indicators weighted by biomass or by abundance should be used to evaluate ecosystem changes. Indicators characterizing size distribution (e.g., slope of size spectrum) appear to be more helpful in distinguishing the cause of ecosystem changes than mean community indicators because their response is specific to the fishing scenario simulated (i.e., global or hake-targeting fishing). Some indicators do not seem to be sensitive to fishing pressure (slope of the diversity size spectrum) or do not vary consistently with other studies (*W* statistic).

Résumé : La sensibilité de plusieurs indicateurs de communauté (basés sur la taille, les espèces ou les niveaux trophiques) est évaluée pour la communauté de poissons de l'écosystème du sud-Benguela (Afrique du Sud), par simulation de scénarios de pêche utilisant le modèle multispécifique OSMOSE. Les simulations suggèrent qu'il peut être erroné de considérer une direction de référence absolue pour un indicateur car la direction de variation d'un indicateur est spécifique à l'assemblage multispécifique considéré ainsi qu'au scénario de pêche simulé. L'analyse des indicateurs spécifiques comparés à ceux de communauté permet de comprendre quels processus sont à l'origine des propriétés émergentes de l'écosystème. Renseignant sur la structure et l'état de l'écosystème, les indicateurs pondérés par la biomasse et ceux pondérés par l'abondance devraient être utilisés ensemble pour évaluer les perturbations de l'écosystème. Les indicateurs caractérisant la distribution en taille (e.g., pente du spectre de taille) semblent plus utiles pour distinguer la cause des changements écosystémiques que les indicateurs de communauté moyennés, car ils varient différemment selon le scénario de pêche simulé. Certains indicateurs semblent ne pas être sensibles à la pression de pêche (pente du spectre de diversité) ou ne varient pas de manière cohérente avec d'autres études (*W* statistic).

Introduction

The need to move towards an ecosystem approach to fisheries (EAF) is now widely recognized. It was first underlined in the 1982 United Nations (UN) Convention on the Law of the Sea and then reinforced with the Food and Agriculture Organization (FAO) Code of Conduct for Responsible Fisheries in 1995 (FAO 1995). Thereafter, the purpose of the Reykjavik Conference (November 2001) was to review the available knowledge about marine ecosystem issues, to identify means by which ecosystem considerations could be included in fisheries management, and to identify future challenges and strategies (Sinclair and Valdimarsson 2003). Finally, the World Summit on Sustainable Development in Johannesburg (2002) advocated the implementation of an EAF before 2010 (Garcia et al. 2003).

Implementing an EAF requires fishing impacts on marine ecosystems to be quantified (Garcia and Staples 2000). Goñi (1998) considered two kinds of fishing impacts: direct impacts on the abundance and demographic structure of target and associated species and on the structure of marine habitats and indirect impacts of fishing on community structure through predation and competition. Jackson et al. (2001) showed that fishing represents the most destabilizing factor for marine ecosystems.

The development and use of ecosystem indicators are needed to evaluate ecosystem health or state and its evolution under fishing pressure. Numerous indicators have al-

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Table 1. Population indicators.

Indicator	Notation	Description	Units	Key references
Mean body length	$\overline{L_i}$	$\overline{L_i} = \frac{1}{N_i}\sum_{N_i} L$	cm	Haedrich and Barnes (1997); Babcock et al. (1999)
Mean body length in catches	$\overline{L_{C_i}}$	$\overline{L_{C_i}} = \frac{1}{C_i}\sum_{C_i} L$	cm	Rochet and Trenkel (2003)

Note: L, fish body length; $\overline{L_i}$, the mean body length of species i; N_i, species abundance without age-class 0; C_i, the number of fish of species i in the catches.

ready been proposed and studied empirically and theoretically (Rochet and Trenkel 2003; Cury et al. 2005; Shin et al. 2005). The Scientific Committee on Oceanic Research / Intergovernmental Oceanographic Commission (SCOR/IOC) symposium "Quantitative Ecosystem Indicators for Fisheries Management" held in Paris in April 2004 (www.ecosystemindicators.org; Daan et al. 2005) reviewed studies about ecosystem indicators, and it appears that there are many indicators, probably with some redundancy, that can be used to evaluate fishing impacts on ecosystems (Daan et al. 2005).

The aims of this paper are to study the sensitivity of a set of ecological indicators to fishing, to compare different kinds of indicators, and to help in selecting a few indicators containing most of the information. To be better able to interpret the variations in some indicators, a simulation approach is adopted based on the application of the individual-based model OSMOSE (Shin and Cury 2001, 2004; Shin et al. 2004) to the southern Benguela ecosystem, South Africa, during the 1990s. Different fishing scenarios and levels of fishing mortality are simulated so as to analyse changes in the indicators in a wide range of possible configurations of the southern Benguela ecosystem.

Materials and methods

Indicators

The sensitivity to fishing of a selection of the main ecological indicators reviewed during the SCOR/IOC symposium (Daan et al. 2005) is evaluated in the southern Benguela ecosystem. Three main categories of ecological indicators are considered in this study: size-based, species-based, and trophodynamic indicators (Tables 1 and 2). They were chosen according to their common use, their ecological meaning, and their theoretical sensitivity to fishing pressure.

Size-based indicators

Fish body size is a life history trait involved in many ecological processes such as respiration, production, survival, growth, and reproduction (Peters 1983; Jennings et al. 2001). Thus size may structure fish communities, notably by its role in predator–prey relationships (Sheldon et al. 1977; Cohen et al. 1993; Shin and Cury 2001). Many species-level and community-level indicators based on fish size have been observed to be sensitive to fishing pressure (Shin et al. 2005).

Mean size

Fishing is size selective, so the mean fish size of a species may vary under fishing pressure (Haedrich and Barnes 1997; Babcock et al. 1999). A reduction in the mean size of a species can be explained by a decrease in the abundance of the large targeted fish and (or) strong recruitment. By contrast, a decrease in the mean size of fish in catches would only reflect a decrease in the abundance of large fish, i.e., recruited fish. Rochet and Trenkel (2003) proposed to extend this indicator to the community level, assuming that the mean size of fish in a community is affected by fishing in the same way as the mean size of fish for a species.

Mean maximum size of a community

The mean maximum size at the community level is derived from the length at infinity for each species, i.e., the Von Bertalanffy parameter L_∞, weighted by the relative abundance of each species. As it is calculated with a fixed species size, it reflects the proportion in abundance of large and small fish species in the ecosystem. Jennings et al. (1999) showed that an increase of fishing pressure on demersal fish in the North Sea can be detected by a decrease of this indicator.

Size spectrum

First studied in the 1970s (Sheldon et al. 1972), the size spectrum corresponds to the distribution of the abundance or biomass of organisms according to their size across a range of phyla. The size spectra of several fish communities were examined (Pope and Knights 1982; Rice and Gislason 1996; Bianchi et al. 2000), and it appears that when represented on a log scale, the size spectrum can be approximated by a decreasing linear function if small size classes are not included (Shin and Cury 2004). The size spectrum is then characterized by its slope, which has been shown to increase (in absolute value) under fishing pressure (Rice and Gislason 1996; Gislason and Rice 1998). When small size classes are included, the size spectrum is sometimes better fitted by a quadratic curve (Bianchi et al. 2000; Shin and Cury 2004), which can be characterized by its curvature. Using a simulation approach, Shin and Cury (2004) suggest that both slopes and curvature can track changes in fishing mortality. In this study, linear regressions are applied to size spectra when small fish (size <20 cm) are excluded from the distribution, and quadratic regressions are applied when small fish are considered.

Species-based indicators

The relative abundance of species, also called evenness, may provide information about changes in ecosystem structure (Greenstreet et al. 1999) and reflects variations in species dominance. Because fisheries are relatively species-

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Table 2. Community indicators.

Indicator	Notation	Description	Key references
Mean body length	$\overline{L}$	$\overline{L} = \sum_i \overline{L_i} \cdot \frac{N_i}{N}$ (cm)	Rochet and Trenkel (2003)
Mean maximum body length	$\overline{L(\max)}$	$\overline{L(\max)} = \sum_i L_{\infty,i} \cdot \frac{N_i}{N}$ (cm), where $L_{\infty,i}$ is the length at infinity in the von Bertalanffy growth model	Jennings et al. (1999)
Size spectrum			
Slope	β	$\ln(N_k) = \alpha + \beta \ln\left(\frac{L_k + L_{k-1}}{2}\right)$	Rice and Gislason (1996); Gislason and Rice (1998); Bianchi et al. (2000); Shin and Cury (2004)
Curvature	γ	$\ln(N_k) = \alpha + \beta \ln\left(\frac{L_k + L_{k-1}}{2}\right) + \gamma\left[\ln\left(\frac{L_k + L_{k-1}}{2}\right)\right]^2$ where k the size-class index	
Shannon–Wiener index	H'	$H' = -\sum_i \frac{N_i}{N} \cdot \log \frac{N_i}{N}$	Magurran (1988)
Slope of diversity size spectrum	β_{DS}	$\log(H') = \alpha_{DS} + \beta_{DS}\left(\frac{L_k + L_{k-1}}{2}\right)$, where k the size-class index	Rice and Gislason (1996); Gislason and Rice (1998)
W statistic (area between biomass and abundance curves in an ABC representation)	W statistic	$W = \sum_{i=1}^{S} \frac{B_{\text{cum},i} - N_{\text{cum},i}}{50(S-1)}$, where B_{cum} is the cumulative biomass and N_{cum} is the cumulative abundance	Yemane et al. (2005)
Mean trophic level	$\overline{\text{TL}}$	$\overline{\text{TL}} = \sum_i \text{TL}_i \cdot \frac{B_i}{B}$, where TL_i is the species trophic level	Pauly et al. (2001)
Fishing-in-balance index	FiB	$\text{FiB} = \log \frac{Y_i}{\text{TE}^{\text{TL}_i}} - \log \frac{Y_0}{\text{TE}^{\text{TL}_0}}$, where trophic efficiency (TE) here equals 0.1	Pauly et al. (2000)

Note: $\overline{L_i}$, mean body length of species i; N_i, abundance of species i without age-class 0; N, total abundance of the community without age-class 0; C, the number of fish in the catches; Y, biomass of fish in the catches; p_i, the proportion in abundance of species i in the community; B_i, the biomass of species i; S, the number of species in the community.

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selective, but also induce indirect effects on nontargeted species, such indicators may be sensitive to fishing pressure.

Shannon–Wiener index

The Shannon–Wiener index (H') is a mixed indicator providing information about both species richness and species evenness (Magurran 1988). The distribution of H' according to fish body size has also been studied, but the diversity size spectrum (DSS) has not been proven to react in a consistent way to fishing pressure (Rice and Gislason 1996; Gislason and Rice 1998). In this study we represent the diversity spectra by the logarithm of H' per size class, which provides a good linear fit.

Abundance biomass comparison (ABC)

Species dominance can be studied by means of *k*-dominance curves, which were first proposed by Lambshead et al. (1983). In this representation, species are ranked according to abundance or biomass on the *x* axis (logarithmic scale), with percentage dominance on the *y* axis (cumulative scale). Warwick (1986) and Clarke and Warwick (1994) suggested the comparison between biomass and abundance dominance curves, called abundance–biomass comparison (ABC), for detecting disturbance in the ecosystem. The area between the two curves, also called the W statistic, is evaluated in this study.

Trophodynamic indicators

The food web is assumed to reflect the main interactions between individuals in a fish community. Furthermore, the reported "fishing down marine food webs" effect (Pauly et al. 1998, 2000) gives incentives to quantify the response of trophodynamic indicators to fishing.

Mean trophic level of the community

The trophic level (TL) is a well-documented indicator of ecosystem structure (Pauly et al. 1998, 2001; Cury et al. 2005). The mean trophic level is calculated by the average of species' trophic levels weighted by species' relative biomass. Because the TL of a fish may change as it grows, using a fixed mean trophic level per species is an approximation used for highlighting changes in the relative biomass of species (i.e., the contribution of a species to the community) and not changes in the trophic role of species in the food web. The TLs for the fish species of the southern Benguela are available from other modelling studies (Shannon et al. 2003; Table 3).

Fishing-in-balance index

The fishing-in-balance (FiB) index (Pauly et al. 2000) measures whether the biomass of catches is in balance with the ecological cost of fishing at that trophic level, i.e., whether a particular trophic level is overexploited when fisheries expand. Assuming that the trophic efficiency (TE) is the same between trophic levels, this indicator is calculated from the biomass of catches and the mean trophic level of the catch. FiB is maintained at zero when a decrease of the trophic level of the catch is compensated for by an ecologically balanced increase in the catch (and vice versa). FiB increases when a fishery expands or when productivity increases and decreases if the fisheries contract geographically or if the food web collapses.

Table 3. Trophic levels used for calculating the mean trophic level (TL) of the community.

Species	TL_i
Anchovy (*Engraulis encrasicolus*)	3.5
Chub mackerel (*Scomber japonicus*)	3.9
Shallow-water hake (*Merluccius capensis*)	4.25
Deep-water hake (*Merluccius paradoxus*)	4.2
Horse mackerel (*Trachurus trachurus capensis*)	3.65
Kingklip (*Genypterus capensis*)	4.5
Lanternfish (*Lampanyctodes hectoris*)	3.6
Lightfish (*Maurolicus muelleri*)	3.6
Round herring (*Etrumeus whiteheadi*)	3.6
Sardine (*Sardinops sagax*)	3
Silver kob (*Argyrosomus inodorus*)	4.5
Snoek (*Thyrsites atun*)	3.6

Note: Trophic levels of the species are from an Ecopath model of the southern Benguela ecosystem during the 1990s (Shannon et al. 2003).

All the indicators presented in this study can be distinguished according to the way in which they are calculated. We distinguish first-order indicators, e.g., mean and mean maximum sizes, the Shannon diversity index, the mean trophic level, and the FiB index, as those that are calculated by just aggregating data. The second-order indicators (indicators characterizing the size spectra, size diversity spectra, and ABC representation) are defined as indicators calculated from complete distributions of community abundance or biomass (along size classes or species ranks).

The multispecies model OSMOSE

The individual-based model OSMOSE is based on the hypothesis that predation is an opportunistic process depending on relative body sizes and the spatiotemporal co-occurrence of a predator and its prey. This size-structured spatial model deals with the main processes of fish life cycle: predation, growth, reproduction, and mortality. The basic unit of the model is the fish school or "super-individual", defined as a group of fish from the same species that have the same size and spatial coordinates and require similar food. The model is structured by means of different classes, with each fish school belonging to a "cohort" class, which in turn belongs to a "species" class. This hierarchical structure allows output variables to be tracked at different levels of aggregation (Shin and Cury 2001, 2004).

The time step adopted for the application of OSMOSE to the southern Benguela ecosystem is a 6-month period (January–June, July–December), corresponding to a compromise between the need to take into account seasonal variations (e.g., migration of fish) and the available data. Fish schools move in a two-dimensional grid divided into square cells (40 cells × 40 cells) with closed boundaries, in this study the southern Benguela ecosystem extending from the vicinity of the mouth of the Orange River (25°40′S, 16°E) to east of East London (37°40′S, 28°E).

Carrying-capacity constraint

In OSMOSE, the carrying capacity corresponds to the upper limit of the total biomass of nonpiscivorous fish, which can include not only larval and juvenile stages, but also adult fish. At the beginning of each iteration, and locally in each

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cell, the biomass of nonpiscivorous fish is compared with the carrying capacity. If this biomass exceeds the carrying capacity, it is reduced in proportion, causing mortality for nonpiscivorous fish. Furthermore, additional mortality is added into the model for larval and juvenile stages (classes of age 0) to account for the higher natural mortality they undergo (Shin et al. 2004) and serves as a tuning parameter for applying the model to the southern Benguela ecosystem.

Foraging and predation

These stages are only applied to piscivorous fish in the model (Fig. 1). School displacement is directed by the search for the adjacent cell with the highest biomass of potential preys. Once it has moved, each piscivorous fish school feeds on fish groups of a suitable size, causing an explicit predation mortality for each fish school preyed upon. At the end of this stage, predation efficiency is calculated for each fish school. This coefficient is determined by the ratio between the food biomass ingested by a school and the food biomass required for the predator to fulfil its vital functions.

Growth and starvation mortality

Mean growth rates in length of fish are calculated from the von Bertalanffy model. This rate is readjusted according to the amount of food ingested by each fish school during each time step. If the predation efficiency is above a critical value, the growth rate in length increases linearly with the predation efficiency. If it is below this critical predation efficiency, the food ration is too low to provide the basic maintenance requirements of fish. In this case, fish schools are affected by starvation mortality, which increases when the predation efficiency decreases. Details are provided by Shin and Cury (2001, 2004).

Fishing mortality

Using Pope's approximation (Pope 1976), fishing mortality is applied to the different species at the middle of the year, i.e., between the January–June and July–December semesters. Because fish catches are simulated uniformly across the spatial grid, the spatial distribution of fishing effort is not taken into account in this model.

Reproduction

At the end of the year, reproduction of fish is simulated by adding a certain number of eggs per species into the system. The number of eggs spawned per species is calculated assuming that the sex ratio is 1:1 and based on input parameters such as the relative fecundity of the species and its age at maturity (Table 4).

Parametrization of the model for the southern Benguela ecosystem

According to their importance in terms of biomass, catches, and food consumption (as it is linked to species interactions), 12 fish species have been selected to represent the southern Benguela fish community: anchovy (*Engraulis encrasicolus*); sardine (*Sardinops sagax*); round herring, also called redeye (*Etrumeus whiteheadi*); horse mackerel (*Trachurus trachurus capensis*); chub mackerel (*Scomber japonicus*); shallow-water Cape hake (*Merluccius capensis*); deep-water Cape hake (*Merluccius paradoxus*); kingklip (*Genypterus capensis*); snoek (*Thyrsites atun*); silver kob (*Argyrosomus inodorus*); lanternfish (*Lampanyctodes hectoris*); and lightfish (*Maurolicus muelleri*). This set contains pelagic and demersal species, representing at least 76.2% of the biomass and 93.8% of the catch of all fish species, according to a study using an Ecopath model of the southern Benguela ecosystem during the 1990s (Shannon et al. 2003). In terms of consumption, these species are responsible for at least 84% of the total consumption by fish species and top predators and 72% of the consumption of small pelagic fish production (Shannon et al. 2003). Furthermore, these 12 species are representative of functional groups. For example, anchovy, sardine, and round herring constituted 97% of the biomass and 99.9% of the catch of small pelagic fish in the 1990s (Shannon et al. 2003). Hake, horse mackerel, kingklip, snoek, and chub mackerel represented about 70% of the biomass of commercially important demersal fish species surveyed in 2001 on the western and southern coasts of the

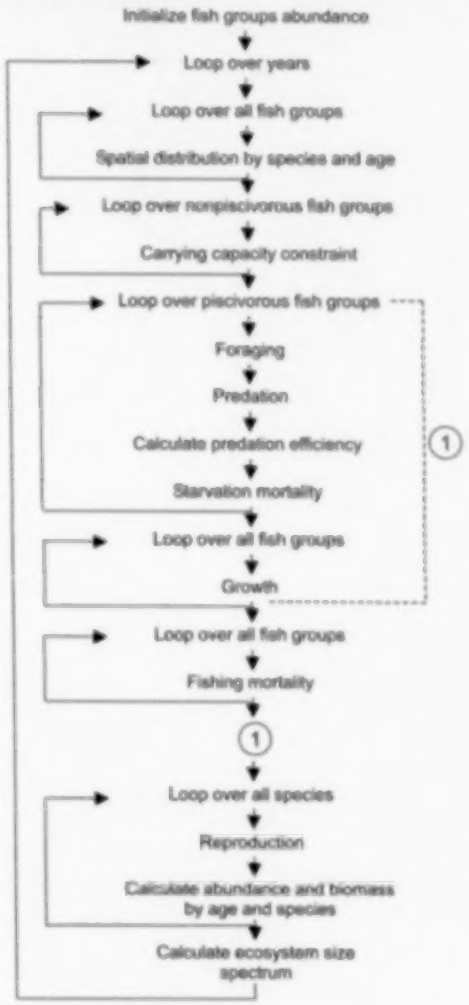

Fig. 1. Process diagram of the OSMOSE model. Processes modelled in a simulated year are presented chronologically (from Shin and Cury 2001).

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Table 4. Input parameters of OSMOSE model for the 12 fish species modelled explicitly.

	Growth				Reproduction		Survival				Initialization
Species	L_∞ (cm)	k (year^{-1})	t_0 (years)	c (g·cm^{-3})	Φ (eggs·g^{-1})	a_{mat} (years)	a_{max} (years)	a_{rec} (years)	M_{add} (year^{-1})	F (year^{-1})	B_{1990s} (tonnes)
Anchovy (*Engraulis encrasicolus*)	14.8	1.37	−0.03	0.007	8000	1	5	1	0.403	0.23	786 143
Chub mackerel (*Scomber japonicus*)	68	0.207	−0.98	0.005	300	3	8	2	0.143	0.07	100 000
Shallow-water hake (*Merluccius capensis*)	270.6	0.039	−0.73	0.005	500	4	15	3	0.228	0.23	388 900
Deep-water hake (*Merluccius paradoxus*)	219.4	0.049	−0.914	0.005	500	4	15	3	0.174	0.33	647 900
Horse mackerel (*Trachurus trachurus capensis*)	54.5	0.183	−0.65	0.009	250	3	8	2	0.314	0.06	532 800
Kingklip (*Genypterus capensis*)	180	0.105	0.05	0.001	500	5	24	3	0.182	0.11	11 583
Lanternfish (*Lampanyctodes hectoris*)	7	1.66	0.06	0.008	646	0.5	2	1	0.226	0.0003	1 126 620
Lightfish (*Maurolicus muelleri*)	6	1.15	0.06	0.008	334	0.5	2	1	0.226	0.0003	1 126 620
Round herring (*Etrumeus whiteheadi*)	30.1	0.71	0.28	0.009	750	1	6	1	0.308	0.04	1 369 720
Sardine (*Sardinops sagax*)	26	0.26	−1.50	0.009	2400	2	10	1	0.365	0.16	460 000
Silver kob (*Argyrosomus inodorus*)	116	0.12	−1.47	0.007	150	2	25	3	0.228	0.181	10 400
Smoothound (*Thyrsites atun*)	115.3	0.294	−0.1	0.018	130	3	10	2	0.132	0.25	74 140

Note: L_∞, k, and t_0 are the parameters of the von Bertalanffy growth model; c is Fulton's condition factor; Φ is relative fecundity; a_{mat} is age at maturity; a_{max} is longevity; a_{rec} is age of recruitment; M_{add} is an additional mortality rate (resulting from predation by other species of the ecosystem that are not explicitly modelled); F is the annual fishing mortality rate; and B_{1990s} is the mean biomass for the 1990s. Values reported in the table come from literature (see Appendix A).

Benguela ecosystem and 90% of the reported demersal commercial catch over the period 1992–1999 (F. Le Clus, Marine and Coastal Management, Private Bag X2, Rogge Bay 8012, South Africa, personal communication, 2002).

At model initialization, these 12 species are created from a number of input parameters (Table 4): survival parameters such as longevity, fishing mortality rates, and age of recruitment; growth parameters such as von Bertalanffy model parameters and Fulton's condition factor; and reproductive parameters such as age at maturity and relative fecundity. Initial abundances of fish are those used or estimated in an application of an Ecopath model of the southern Benguela during the 1990s (Shannon et al. 2003) (Table 4). The spatial distributions of each species by age class and by semester are given in Travers et al. (2004). The tuning of the model was undertaken by allowing larval mortalities to vary in order to obtain mean species biomasses in the range estimated for the 1990s (Shannon et al. 2003).

Simulations

Fishing scenarios

To test the sensitivity of indicators to fishing pressure, different fishing scenarios are simulated. Each scenario is run 25 times for 200 years, and only the 100 last years of each simulation are kept to calculate the mean of the indicators. The first scenario simulated is an increase of the global fishing mortality, using a multiplier of fishing mortality (mF) for all species ranging from 1 to 2.5, with a step of 0.1. The second scenario corresponds to an increase of the fishing mortality for hakes (shallow and deep water), with a multiplier (mF) ranging from 1 to 2 (value at which both species of hakes collapse), whereas the fishing mortalities of the other species do not change from the reference state. For the third scenario, an increase of the fishing mortality of small pelagic fish, i.e., for sardine, round herring, and anchovy, is simulated (mF from 1 to 2.5). Finally, the fourth scenario corresponds to the development of a mesopelagic fishery targeting lanternfish and lightfish by increasing the fishing mortality (F) of both species from 0 to 1 year^{-1}.

Reference state

To compare the relative variation of indicators in each fishing scenario, a reference state is defined. This reference state is chosen as the simulation of the fisheries state from 1990 to 1997 in the southern Benguela ecosystem. This reference state is also the one used for tuning the model. The OSMOSE model provides output species biomass, species abundance, and species mean size in the ecosystem and in the catches, globally and per size class. From all these outputs, the indicators previously described can be calculated and compared. To compare the sensitivity of the whole set of indicators on the same scale, indicators are graphically presented as the ratio of their value in each scenario to their value in the reference state (initial tuned 1990s model). For the case of the FiB index, the reference value equals 0 by definition. To compare it with the other indicators, FiB values were incremented by 1 to facilitate use of the ratio relative to the reference state for this indicator as well.

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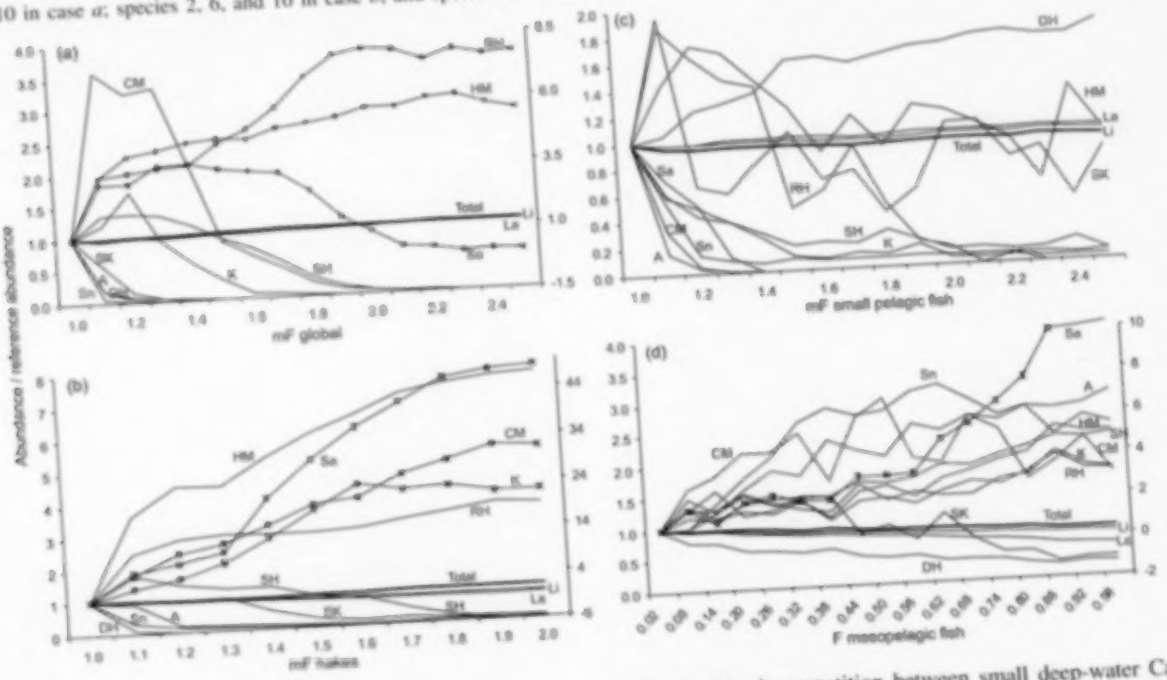
Fig. 2. Relative changes in the abundance of the 12 modelled species in each fishing scenario: (*a*) global scenario, an increase of the fishing mortality for all species; (*b*) hake scenario, an increase of the fishing mortality for deep- and shallow-water hake; (*c*) small pelagic scenario, an increase of the fishing mortality for anchovy, sardine, and round herring; and (*d*) mesopelagic scenario, an increase of the fishing mortality of lanternfish and lightfish. The ratio between the simulated abundance N and the reference abundance N_{ref} is represented for each species against a multiplier of fishing mortality (mF) or against the fishing mortality (F) in the case of the mesopelagic scenario (*d*). Species: A, anchovy (*Engraulis capensis*); CM, chub mackerel (*Scomber japonicus*); SH, shallow water hake (*Merluccius capensis*); DH, deep water hake (*Merluccius paradoxus*); HM, horse mackerel (*Trachurus trachurus capensis*); K, kingklip (*Genypterus capensis*); La, lanternfish (*Lampanyctodes hectoris*); Li, lightfish (*Maurolicus muelleri*); RH, round herring (*Etrumeus whiteheadi*); Sa, sardine (*Sardinops sagax*); SK, silver kob (*Argyrosomus inodorus*); Sn, snoek (*Thyrsites atun*). Total abundance is represented by the thick line. In *a*, *b*, and *d*, curves marked with crosses should be read on the second *y* axis on the right (species 5, 9, and 10 in case *a*; species 2, 6, and 10 in case *b*, and species 10 in case *d*).



Results

Simulations of the fishing scenarios

The relative variations of abundance of each species in each scenario are presented (Fig. 2; relative variations of biomass are very similar). With an increase of the fishing mortality for all species, some of them collapse rapidly (Fig. 2*a*). By contrast, two species (horse mackerel and round herring) seem to take advantage of the ecosystem disturbance and display large increases in abundance. As expected, hake abundance decreases in the second scenario (Fig. 2*b*), but indirect effects of heavy fishing on hake are also observed: the abundance of kingklip, which is a competitor of adult hakes, the abundance of horse mackerel, which is a competitor of juvenile hakes, and the abundance of sardine and round herring, which are prey of hakes and also compete with juvenile hake for zooplankton prey, increase as hake abundance decreases. As expected, the scenario of increased fishing on small pelagic fish (Fig. 2*c*) leads to a decrease in the abundance of anchovy, sardine, and round herring. There is a parallel decrease in the abundance of most other species. However, despite a decrease in small pelagic fish, which are prey for hake, deep-water Cape hake shows a marked increase, possibly as a result of reduced competition between small deep-water Cape hake and other fish species, particularly small pelagics. In addition, the small relative increase in mesopelagic abundance (+1.5%), which are the main prey for deep-water hake, corresponds to an absolute increase that is not negligible (+7526 millions of individuals) because initial biomass and abundance of mesopelagics is by far the highest of the species modelled (Table 4). The mesopelagic fish scenario (Fig. 2*d*) illustrates well the bottom-up effect of this fishing configuration. Indeed, the increased fishing mortality on mesopelagic fish, which have a low trophic level, decreases their abundance, which in turn causes abundance of top predators such as deep-water Cape hake and silver kob to decline. In contrast, the abundance of competing species such as small pelagic fish (e.g., anchovy and sardine) and predators relying heavily on the latter forage fish species (e.g., snoek) increases greatly.

Sensitivity analysis

Species indicators

Species indicators help to explain the response of community indicators to increasing fishing mortality (presented in

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Fig. 3 for the global scenario). Contrary to theoretical predictions, the mean size of the fish community increases with global fishing mortality (Fig. 3*a*). This trend can be explained by the increase in mean size of large fish such as kingklip and shallow-water Cape hake (Fig. 3*a*) but above all by the strong decrease in the abundance of some small-sized fish species that were dominant in the initial reference state, e.g., anchovy (Fig. 2*a*). The increase in the mean size of the community in catches, despite the decline in the mean sizes of all species (Fig. 3*b*), confirms that the increase of this indicator in catches and in the ecosystem is mainly due to a decrease in abundance of small-sized fish species that are commercially exploited.

First-order community indicators

First-order indicators do not vary in the same direction and with the same amplitude in the four fishing scenarios (Fig. 4). The mean size in the community decreases in the small pelagic fish scenario (Fig. 4*c*), whereas it increases in the three other scenarios (Figs. 4*a*, 4*b*, 4*d*). The mean maximum size of fish in the catch responds with large amplitude in the small pelagic fish scenario (Fig. 4*c*), whereas it varies only slightly in the hake scenario (Fig. 4*b*). It can also be noted than first-order indicators in the global scenario vary in a similar way to indicators in the hake scenario (Figs. 4*a* and 4*b*), whereas their variations are very different from those in the small pelagic and mesopelagic fish scenarios. On the other hand, some indicators appear to vary concomitantly in all scenarios. For example, the mean size and the mean maximum size (either in the ecosystem or in catches) have the same direction of change in each fishing scenario considered (Fig. 4). It can be noticed that, in all cases, mean maximum size is more sensitive to fishing mortality than mean size. The Shannon index H' also varies in a similar way to mean and mean maximum size in the ecosystem. By contrast, the mean trophic level does not seem to vary like other first-order indicators. Furthermore, its amplitude of variations is generally smaller than those for the other indicators. Finally, the FiB index reacts differently to increased fishing: FiB increases in the small pelagic and mesopelagic scenarios and shows two directions of variation according to the intensity of fishing for the global and the hake scenario, declining when F increases are low and increasing again as F increases further. The latter trajectories appear to mirror the trajectories followed by the maximum lengths of fish in catches in the global and hake scenarios.

The sensitivity of these indicators should be treated with care and considered in relation to the way in which they are weighted. In the mesopelagic fish scenario, for example, the decrease in the mean and mean maximum size in catches must be related to the large increase of mesopelagic fish catches, as these indicators are weighted by abundances.

Second-order community indicators

Second-order indicators, or indicators calculated from distributions, are presented for the four scenarios (Fig. 5). They show large amplitudes of variation, particularly the curvature of the quadratic size spectrum. In each scenario, the slope of the size spectrum (estimated from a linear regression) varies more or less linearly with fishing mortality, as already shown by other studies (Gislason and Rice 1998; Shin and Cury 2004). The curvature estimated by a quadratic fit of the size spectrum varies with a higher amplitude than the slope for each scenario. However, its response curve to fishing is more difficult to interpret (particularly in the global scenario; Fig. 5*a*). The indicator W statistic displays the same direction of variation in all four scenarios: it decreases in relative value (increases in real values as W statistic takes negative values in the simulations) when the fishing mortality increases.

Diversity size spectra are fitted by a straight line, with a high determination coefficient ($0.88 < R^2 < 0.97$ for the four scenarios) compared with the regressions made in some empirical studies (e.g., Gislason and Rice 1998; Bianchi et al. 2000). However, the slope of the diversity size spectrum does not vary significantly with fishing mortality (Student's t test: p value = 0.052 for the global scenario, 0.33 for the hake scenario, 0.77 for the small pelagic scenario, and 0.097 for the mesopelagic scenario). Therefore, this indicator is considered not to be sensitive to fishing.

Fig. 3. Mean size for the global scenario in (*a*) the ecosystem and (*b*) catches ($\overline{L_c}$). The ratio between the simulated mean size ($\overline{L_c}$) and the reference mean size ($\overline{L_c}$(ref)) is represented for the 12 species (A, anchovy (*Engraulis capensis*); CM, chub mackerel (*Scomber japonicus*); SH, shallow water hake (*Merluccius capensis*); DH, deep water hake (*Merluccius paradoxus*); HM, horse mackerel (*Trachurus trachurus capensis*); K, kingklip (*Genypterus capensis*); La, lanternfish (*Lampanyctodes hectoris*); Li, lightfish (*Maurolicus muelleri*); RH, round herring (*Etrumeus whiteheadi*); Sa, sardine (*Sardinops sagax*); SK, silver kob (*Argyrosomus inodorus*); Sn, snoek (*Thyrsites atun*)) and for the community ($\overline{L_c}$). The mean size of the community in catches should be read on the second y axis on the right. A stop in the line of a species mean size means the species collapses.

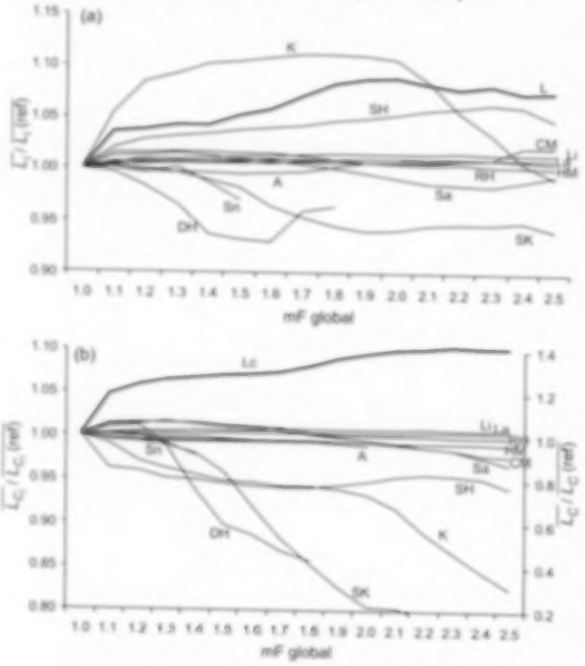

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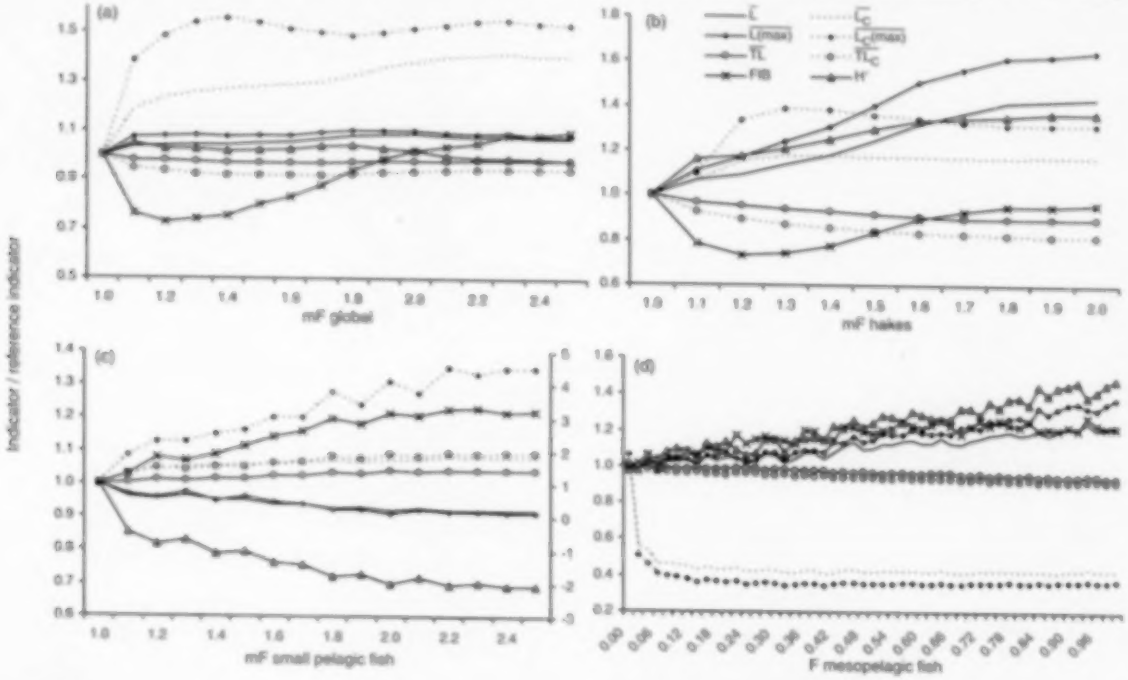
Fig. 4. First-order indicators for each scenario: (*a*) global; (*b*) hake; (*c*) small pelagic fish; and (*d*) mesopelagic fish. Indicators are represented as a ratio between the simulated indicator value and its reference value. $\overline{L}$ is the mean size in the ecosystem, $\overline{L_C}$ is the mean size in catches, $\overline{L(\max)}$ is the mean maximum size in ecosystem, $\overline{L_C(\max)}$ is the mean maximum size in catches, $\overline{\mathrm{TL}}$ is the mean trophic level in ecosystem, $\overline{\mathrm{TL}_C}$ is the mean trophic level in catches, FiB is the fishing-in-balance index incremented of 1, and H' is the Shannon diversity index. In the small pelagic fish scenario (*c*), $\overline{L_C}$ and $\overline{L_C(\max)}$ should be read on the second *y* axis on the right.



Discussion

Community indicators vs. species indicators

When simulating a global increase of the fishing mortality of all species, community indicators and species indicators do not vary in the same direction and with the same amplitude. These indicators do not reflect the same processes, but they are often correlated, notably by the way in which community indicators are calculated. In our simulations, the mean length of fish in the southern Benguela fish community displays a direction of change that is opposite to the direction expected on theoretical grounds or to the observed direction in specific communities, e.g., demersal (Rochet and Trenkel 2003; Shin et al. 2005). This result highlights the fact that community indicators reflect nontrivial properties, which emerge from complex and hardly predictable species interactions. Therefore, they must be analysed in parallel with population indicators for understanding underlying processes. Because the mean size of the community is calculated by the weighted average of the mean size of the species, the increase of this community indicator can be explained either by variations of species indicators or by variations of the relative abundances of small and large species. In the ecosystem, with a simulated increase of the global fishing mortality, the increase of the mean length of the community seems to be caused by the collapse of species with a small mean size (e.g., anchovy which was initially abundant), counterbalanced by a relatively large increase in abundance of species a little larger (e.g., round herring and horse mackerel). Moreover, the increase of the mean length of the community is also due to the increase in the mean size of large species such as kingklip and shallow-water Cape hake. Therefore, variations of length at a species level can involve variation of the size structure of the community.

Indicators in the ecosystem and in catches

Indicators in catches and in ecosystems do not have the same sensitivity and may not even change in the same directions. Indicators in catches concern only recruited stages, whereas indicators in the ecosystem would reflect the whole population, including prerecruit stages. By comparing variations of indicators in the ecosystem and in catches, the respective role of recruits and prerecruits (and beyond this simulation framework, targeted versus nontargeted fish species or size classes) can be better understood. As an example, in the global scenario, the decreasing mean size of kingklip in catches allows us to understand that the increase in the mean size of kingklip in the ecosystem is either due to a decrease in the abundance of prerecruited stages (recruitment overfishing as an indirect effect of fishing) or to a larger size at age of prerecruits. Indicators in catch are complementary to indicators in the ecosystem because they highlight which part of the life cycle of a species is responsible for changes in the indicators. Furthermore, the interplay be-

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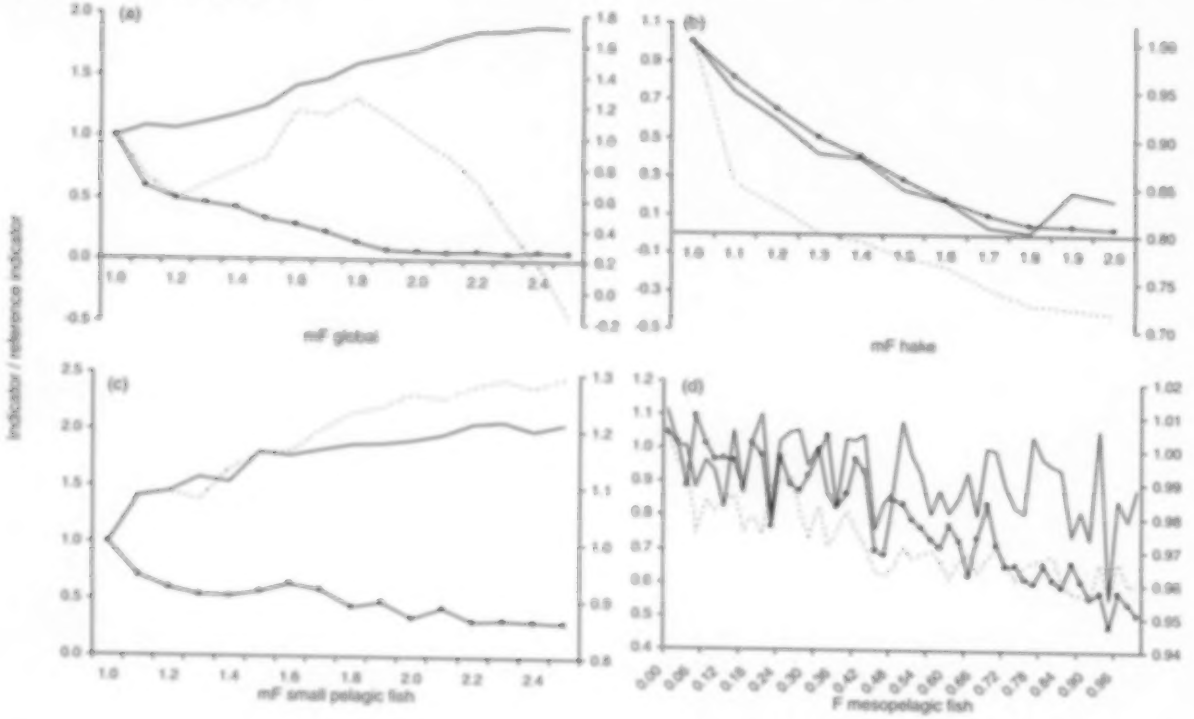
Fig. 8. Second-order indicators for each scenario: (*a*) global; (*b*) hake; (*c*) small pelagic fish; and (*d*) mesopelagic fish. The slope is estimated by fitting a linear curve to the size spectra, curvature is estimated by fitting a quadratic curve to the size spectra. Indicators are represented by the ratio between the simulated value and the reference value. The slope of the size spectra should be read on the second *y* axis to the right. Broken line, curvature of the quadratic size spectrum; solid line with solid circles, *W* statistic; solid line, slope of the linear size spectrum.



tween targeted and nontargeted species would be captured by the comparison between indicators in ecosystem and in catch, but it is not simulated here because all species included in the model are subject to fishing.

First-order indicators and weightings with abundance or biomass

For each scenario, many of the first-order indicators vary in the same way. For example, trophic levels in the community and in catches show similar levels of sensitivity to fishing, and mean size and mean maximum size vary in similar ways, with only a slight difference in amplitude. Conversely, relative changes in the mean trophic level are not in the same direction or of the same magnitude as the mean maximum size, whereas both indicators are expected to capture the variations in the proportion of large (high trophic level) and small (low trophic level) species (Cury et al. 2005; Shin et al. 2005). The differences or similarities in behaviour of some indicators can be explained by the weighting used for their calculation rather than by their ecological meaning. Mean size, mean maximum size, and the Shannon diversity index are weighted by abundances, whereas mean trophic level is weighted by biomass. The FiB index does not vary in the same way as the trophic level in the catch. It is the only first-order indicator that still continues to change after the global m*F* exceeds 1.8, probably because it takes into account the global biomass and is not calculated as a simple weighted average as the other first-order indicators. Thus, depending on the way in which weighting is done, community indicators show similar or different trends. Therefore, when evaluating fishing effects, it is important to track changes in at least two types of indicators weighted differently. It should be noted that the weighting by abundance could hide some processes by overweighting some small-sized species, like mesopelagic fish, which are very abundant in the Benguela ecosystem. Similarly, in other studies, fishing effects may be masked by underweighting of larger-sized species that are present at high biomass levels.

The comparison of the indicators weighted by abundance suggests that variation of the mean size in the community is mostly due to variation of the relative abundances of species (rather than to variations in the mean size of the species), as is the case for the mean maximum size of the community, which is calculated from fixed maximum size of the species. For the four scenarios, fishing effects at the level of the community appear to be more interspecific than intraspecific. Because diversity (H') and size-based indicators (L and $L(\max)$) vary in the same way within a given scenario, they could be considered as being redundant in the frame of these simulations, simply reflecting changes in the relative abundances of the species. However, in some other configurations, mean length and mean maximum length of the

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community should help discriminate between variations in length resulting from inter- or intra-specific changes.

Second-order indicators

As predicted by theory and reported in empirical studies (see review in Shin et al. 2005), the slope of the size spectrum increases in absolute value with increasing fishing mortality in the global scenario. As in other modelling studies (Gislason and Rice 1998; Shin and Cury 2004), the slope varies linearly with fishing mortality but with a smaller amplitude for the three other scenarios than for the global one. The curvature of the size spectrum responds with a larger amplitude to fishing mortality. The curvature may be more sensitive to variations in abundance of very small fish in the size spectrum because of the wider size range used in the distribution, including small fish. However, the simulated curvature does not always respond linearly to fishing mortality, which suggests that the interpretation of observed variations in this indicator may be more complicated. For example, in the global scenario, the initial decrease of the absolute value of the curvature (which is negative) until $mF = 1.2$ is attributed to a high abundance of kingklip (the largest species after hakes), which then begins to decrease (where the absolute value of the curvature starts to increase) and collapses at around $mF = 1.7$. The final relative decrease of the curvature can be explained by the delayed decrease in the biomass of sardine. So the curvature of size spectra appears to be informative about the size structure as well as species composition of the fish community. As slope and curvature are not estimated from the same size range (not including and including small size classes, respectively), it may be worthwhile tracking both characteristics of size spectra to capture maximum information. Furthermore, contrary to first-order indicators, second-order indicators respond quite differently in the global scenario and in the hake scenario. These indicators may be better adapted than first-order indicators to track changes caused by different fishing configurations.

The response of the W statistic to fishing is equivocal in the simulations. On the one hand, it presents a consistency in its direction of change and is highly sensitive. For all scenarios, the W statistic decreases in absolute value as the fishing mortality increases. However, this response is not as expected from theoretical and empirical studies. Warwick and Clarke (1994) consider the W statistic as an indicator of the degree of disturbance of the ecosystem. In the marine environment, Yemane et al. (2005) show that this indicator calculated for the demersal fish assemblage off South Africa decreases (increases in absolute value) with fishing intensification. The simulation results suggest that the W statistic may have different directions of change according to the community considered. In an ecosystem in which small pelagic fish predominate (as is the case in upwelling ecosystems), this indicator shows an opposite direction of variation to demersal assemblages. Furthermore, because it exhibits a single direction of variation in all fishing scenarios, the W statistic may not provide information on which species are targeted or on which indirect effects fishing may impose on different functional groups. Thus the usefulness of this indicator to evaluate the ecosystem effects of fishing appears to be questionable.

Range of sensitivity

In observing the response of indicators to simulated changes in fishing mortality, it appears that some of them become less sensitive to fishing beyond a certain threshold. For example, in the global scenario, the mean maximum size in catch levels off after the threshold $mF = 1.3$. Conversely, other indicators display a continuous variation, e.g., the slope of the size spectrum, which varies linearly with increasing fishing mortality in the global and in the hake scenario. These latter indicators may be more useful because their response is uniform and they are sensitive over a wide range of fishing mortalities. Simulations allow the range of sensitivity of various indicators to be evaluated and the response curves of indicators to fishing (e.g., linear, existence of a plateau or a dome) to be specified, which is something difficult to address empirically. They can help the selection of relevant indicators in lightly or heavily fished situations.

In conclusion, the comparison of indicators in different fishing scenarios highlights the fact that the same indicators can increase or decrease from the reference state according to which species are strongly exploited. When considering all possible fishing scenarios, there are no consistent reference directions for the indicators under scrutiny, which reflects the fact that the response of the ecosystem to fishing will differ according to which functional groups are targeted. This study shows that indicators do not always vary as theoretically predicted because of indirect effects of fishing on the different components of the ecosystem. Therefore a simulation approach can be useful for better understanding the emergent properties of a particular ecosystem under fishing pressure. When proposing reference directions of change for indicators in an EAF perspective, the fishing configuration (species targeted, fishing intensity) and the type of community studied should be carefully specified. For the southern Benguela upwelling ecosystem, some of the second-order indicators appear to be relatively sensitive to fishing pressure over a wide range of fishing mortality. The exception is slope of the diversity size spectra, which does not appear to be sensitive to changes in fishing mortality. Moreover, they are helpful for differentiating fishing effects between the global and species-specific fishing scenarios, e.g., the hake scenario (whereas first-order indicators vary in the same direction in both the global and the hake scenarios). The use of different kinds of indicators (second-order indicators, first-order indicators weighted by abundance and biomass, species indicators) is required to obtain a complete picture of the ecosystem because the way in which indicators are calculated is informative about ecosystem structure. In addition, the ecosystem dynamics reflect a diversity of processes that can be analysed by means of a combination of diverse indicators such as those studied in this paper: size-based, species-based, and tropsodynamic indicators.

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Appendix A

Table A1 appears on following page.

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Table A1. References of the species parameters used in OSMOSE.

	Growth		Reproduction		Survival		
	L_∞, k, t_0	c	Φ	a_{mat}	a_{max}	a_{inv}	M_{adult}, F, B_{1990s}
Engraulis encrasicolus	Waldron et al. 1989	Van der Westhuizen,* personal communication 2002	*Melo 1994; Le Clus 1979*	Armstrong et al. 1991	Kerstan,*† personal communication 2002	Armstrong et al. 1991	Shannon et al. 2003
Scomber japonicus	Baird 1977	Baird 1977	*Collette and Nauen 1983*	Crawford 1989	Castro Hernández and Santana Ortega 2000	*Crawford 1989*	Shannon et al. 2003
Merluccius capensis	Punt and Leslie 1991	Punt and Leslie 1991	*Kartas and Quignard 1984*	Punt and Leslie 1991	Leslie,* personal communication 2002	Leslie,* personal communication 2002	Shannon et al. 2003
Merluccius paradoxus	Punt and Leslie 1991	Punt and Leslie 1991	*Kartas and Quignard 1984*	*Punt and Leslie 1991*	Leslie,* personal communication 2002	Leslie,* personal communication 2002	Shannon et al. 2003
Trachurus trachurus capensis	Horsten 1999	Kerstan,*† personal communication 2002	*Kartas and Quignard 1984*	Leslie,* personal communication *in* Butterworth and Clarke 1996	Horsten 1999	Hecht 1990	Shannon et al. 2003
Genypterus capensis	Japp 1990; Leslie,* personal communication 2002	Japp 1990	*Hakes relative fecundity*	Japp 1990; Payne and Badenhorst 1989	Japp 1990	*Punt and Japp 1994*	Shannon et al. 2003
Lampanyctodes hectoris	Prosch 1986	*Haimovici and Velasco 2000*	Prosch 1991	Prosch 1986	*Prosch 1986*		Shannon et al. 2003
Maurolicus muelleri	Prosch 1986	*Haimovici and Velasco 2000*	Prosch 1991	Prosch 1986	*Prosch 1986*		Shannon et al. 2003
Etrumeus whiteheadi	Waldron et al. 1991	Geldenhuys 1978	*Baxter and Pope 1969; Kosior and Strzyzewska 1979*	*Roel and Melo 1990*	Kerstan,*† personal communication 2002	*Roel and Armstrong 1991*	Shannon et al. 2003
Sardinops sagax	*Baird 1977; Leslie,* personal communication 2002*	Van der Westhuizen,* personal communication 2002	*Akkers 1995*; Van der Lingen,* personal communication 2004	*Akkers et al. 1996*	Kerstan,*† personal communication 2002	Crawford 1980	Shannon et al. 2003
Argyrosomus inodorus	Kirchner 1998	Griffiths 1996	*Battaglene and Talbot 1994*	Griffiths 1997	Griffiths 1995, 1997	Griffiths 1997	Shannon et al. 2003
Thyrsites atun	*Venidiktova 1958*	Griffiths,* personal communication 2002	*Rowling 1994; Nakamura and Parin 1993*	Griffiths 1999	Griffiths 1999	Griffiths,* personal communication 2002	Shannon et al. 2003

Note: Italicized values are estimated or adapted by the authors based on cited references.
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†Mickael Kerstan died in early 2005.

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